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Big and beautiful: the *Megaxyela* species (Hymenoptera, Xyelidae) of East Asia and North America

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[4] urn:lsid:zoobank.org:author:0D46A0A2-6555-4045-A276-B9539EC54088
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Abstract. *Megaxyela* Ashmead, 1898 comprises 13 species, four of which are described as new and one is removed from synonymy: *Megaxyela euchroma* Blank, Shinohara & Wei sp. nov. from China (Zheijang), *M. fulvago* Blank, Shinohara & Wei sp. nov. from China (Hunan, Jiangsu, Zhejiang), *M. inversa* Blank & D.R. Smith sp. nov. from the USA (West Virginia), *M. langstoni* Ross, 1936 sp. rev. from the eastern USA, and *M. pulchra* Blank, Shinohara & Sundukov sp. nov. from China (Hubei, Jilin, Liaoning, Shaanxi, Tibet), South Korea (Kangwon-do) and Russia (Primorskiy Kray). The male of *M. parki* Shinohara, 1992 is described for the first time. A lectotype is designated for *M. gigantea* Mocsáry, 1909. A cladogram, based on COI sequences of seven species, is presented and interpreted in view of selected morphological characters. Records of *M. fulvago* sp. nov. from Hunan and of *M. pulchra* sp. nov. from Tibet extend the known distribution of *Megaxyela* in the Old World 600 kilometers farther south and 2500 kilometers farther west than previous records.

Keywords. Key, new species, distribution, larval hostplants, COI barcoding.

Introduction

Adults of *Megaxyela* Ashmead, 1898 represent the most colorful and the largest extant xyelids with a body length of up to 14 mm. Despite their conspicuousness, collection records are comparatively seldom. The distribution of the extant species of *Megaxyela* covers the eastern part of the Nearctic and the southeastern part of East Asia (Shinohara 1992; Smith & Schiff 1998; this paper). Outside this area, the Oligocene †*Megaxyela petrefacta* Brues, 1908 was recorded from western North America from deposits of Florissant (Colorado, USA; Brues 1908; Zhelochovtsev & Rasnitsyn 1972). A second fossil species, †*M. yaoshanica* Zhang, 1989 from deposits at Shanwang (Shandong, China) dates back to the mid-Miocene (Zhang 1989). Fossils of *Megaxyela* are young in comparison with the earliest Megaxyelinae from the Upper Jurassic (e.g., Rasnitsyn 1966, 2008; Zhang & Zhang 2000) and the oldest Xyelidae from the Late Triassic (e.g., Kopylov 2014; Lara *et al.* 2014).

Larvae of *Megaxyela* are external feeders of Juglandaceae. The East Palaearctic *M. gigantea* Mocsáry, 1909 feeds on the leaves of *Juglans* Linné and *Pterocarya* Nuttal ex Moquin. Saito (1941) reported on the oviposition behavior of this species. Taeger *et al.* (2010: pl. 21, fig. 3) depicted an unidentified larva found in Yunnan, China, feeding on *J. sigillata* Dode. The Japanese *M. togashii* Shinohara, 1992, which is associated with *J. ailanthifolia* Carrière, represents the first Eurasian species for which the larva and ecological traits have been described in detail (Shinohara *et al.* 2017). The North American *M. aviingrata* (Dyar, 1898), *M. langstoni* Ross, 1936 and *M. major* (Cresson, 1880) have also been found on Juglandaceae like pecan (*Carya illinoinensis* (Wangenh.) K.Koch) and butternut (*Juglans cinerea* L.) (e.g., Dyar 1898a; Smith 1967; Smith & Schiff 1998). *Megaxyela major* has been reported as a minor pest of cultivated pecan trees in Texas (Ree 2012, 2014). Collection circumstances of *Proctorenyxa incredibilis* Kozlov, 1994 on *Juglans mandshurica* Maxim. in the Russian Far East indicate that *Megaxyela* might be the hosts of Proctorenyxidae, an enigmatic family of the parasitic Proctotrupoidea represented by only two species (Lelej 2012; Kim *et al.* 2016).

Five Nearctic and three East Palaearctic species were previously known for the extant fauna (Shinohara 1992; Smith & Schiff 1998). Here, we add four new species, *M. euchroma* Blank, Shinohara & Wei sp. nov., *M. fulvago* Blank, Shinohara & Wei sp. nov., *M. inversa* Blank & D.R. Smith sp. nov. and *M. pulchra* Blank, Shinohara & Sundukov sp. nov., and we remove *M. langstoni* from synonymy. We review *Megaxyela* with focus on the Old World taxa and summarize data on larval hosts and distribution. The analysis of COI barcodes is used to complement morphological studies.

Material and methods

Morphological terminology

Morphological terminology generally follows Huber & Sharkey (1993) and Viitasaari (2002); for surface microsculpture it follows Harris (1979). The elongate and widened third antennal article, which is the ontogenetical product of the fusion of a variable number of articles, is called synantennomere 3 (Fig. 1D; Blank 2002; Blank *et al.* 2005, 2013). The combination of the thinner articles following distally is the antennal filament (Fig. 1D). In *Xyela* and *Pleroneura* the male genitalia are revolved at 180° along their longitudinal axis after ecdysis (strophandrous state), whilst in *Xyelecia*, *Macroxyela*

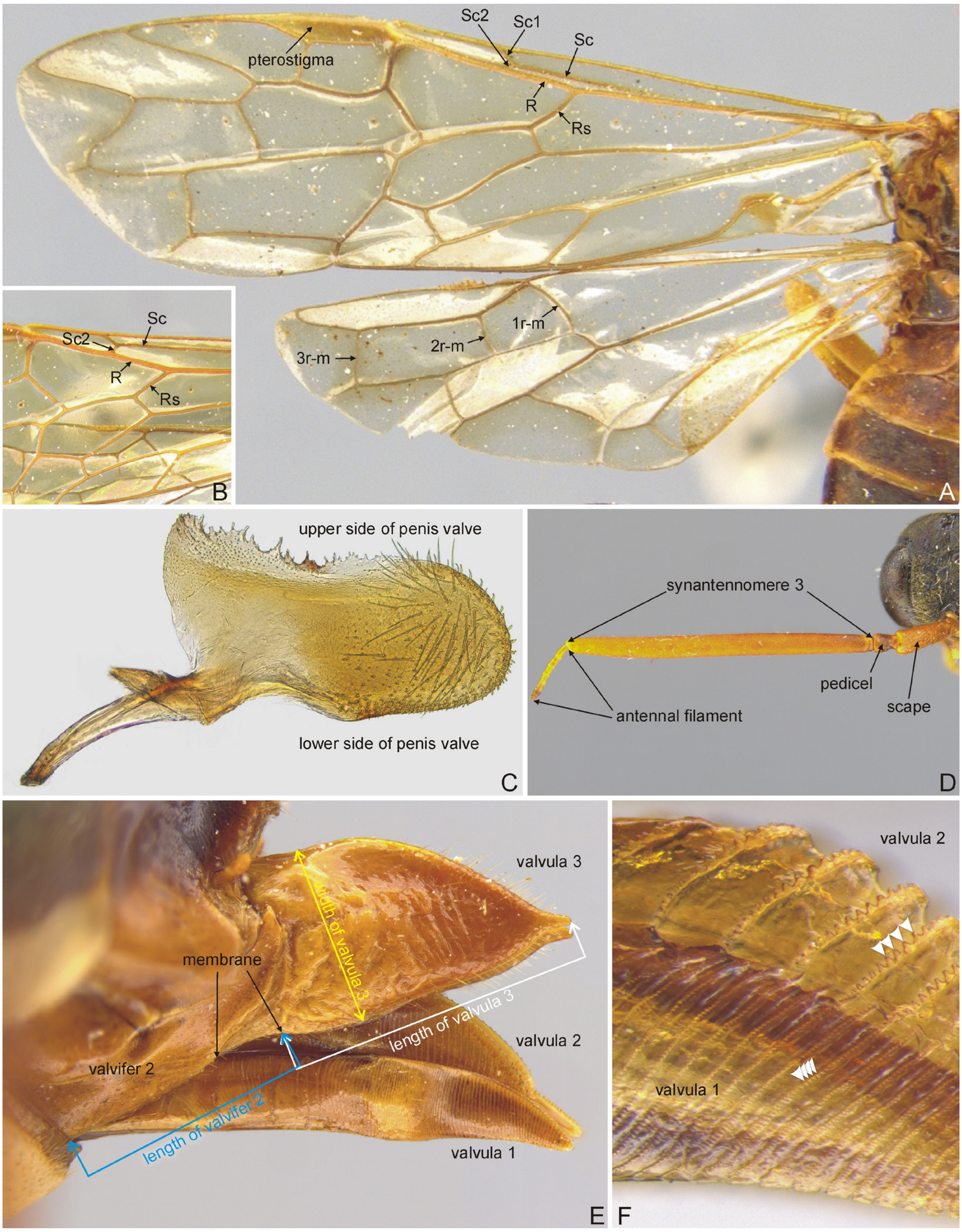

Fig. 1. *Megaxyela* Ashmead, 1898, morphological terminology. **A**. *M. major* (Cresson, 1880) (♀, paralectotype, DEI-GISHym 30823, ANSP), wings. **B**. *M. parki* Shinohara, 1992 (♀, 18509, NSMT), section of fore wing. **C**. *M. euchroma* Blank, Shinohara & Wei sp. nov. (♂, paratype, 22513, NSMT), penis valve. **D**. *M. parki* (♂, 710, NSMT), antenna. **E**. *M. gigantea* Mocsáry, 1909 (♀, holotype of *M. mikado* Sato, 1930, 22350, NSMT), ovipositor and ovipositor sheath, with indication of measurement of length of valvifer 2 (blue), valvula 3 (white), and width of valvula 3 (yellow). **F**. *M. euchroma* sp. nov. (♀, paratype, 22558, CSCS), section of ovipositor, white arrow heads indicating teeth of ctenidia on valvulae 1 and 2.

and *Megaxyela* they remain untwisted in the adult (orthandrous state). To avoid confusion in comparing characters among strophandrous and orthandrous taxa, the penis valves of *Megaxyela* are illustrated with the ventral margin directed upwards as it is usual for most sawflies. Accordingly, the physiological ventral vs. dorsal parts are called upper vs. lower parts of the penis valve (Fig. 1C). Terminology for wing veins as applied here is illustrated in Fig. 1A–B. The ovipositor sheath is composed of the proximal valvifer 2 and the distal valvula 3, which are connected by a membrane (Fig. 1E). Valvula 1 (lancet) is the movable part of the ovipositor situated at rest ventral to valvula 2 (lance) forming the guide for valvula 1 (Fig. 1E–F). Along the annuli of these valvulae, rows of teeth may occur called ctenidia (Fig. 1F; Smith 1968). Ctenidia represent protrusions of the integument, not sensilla trichodea as observed along the annuli in many sawfly species (Blank & Schönitzer 1994).

Measurements

The following measurements have been taken: Length of body: distance between interantennal area and tip of tergum 9+10 in females (ovipositor not included in measurement), between interantennal area and tip of hypopygium in males. Length of fore wing: distance between anterior edge of tegula and distal edge of wing. POL, postocellar line: shortest distance between medial edges of posterior ocelli. OOL, ocellus-ocular line: shortest distance between lateral edge of posterior ocellus and nearest edge of neighboring eye. OCL, ocellus-occipital line: shortest distance between posterior edge of posterior ocellus and posterior edge of head. POL, OOL and OCL are each taken in vertical view on the measured line. Distance of antennal toruli: shortest distance between medial (sclerotized) edges of toruli. Distance between eye and antennal torulus: shortest distance between lateral (sclerotized) edge of torulus and medial edge of eye. Width of frons: distance between medial edges of eyes at level of dorsal edges of antennal toruli. Length and width of eye: longest distance between dorsal/ventral and medial/posterior edge of eye in obliquely lateral view (respective edges in same focus plain). Length of malar space: shortest distance between ventral edge of eye and edge of mandibular concavity. Number of articles of antennal filament: completely and incompletely separated articles counted as single articles. This applies in particular to the distal two articles that are sometimes separated by a suture on the posterior/anterior side but continuous anteriorly/posteriorly. More rarely, malformed articles with partial separation occur in the medial section of the filament. Length of synantennomere 3, antennal filament, article 3 of maxillary palp, metafemur, metatibia, longer metatibial spur: distance between proximal and distal end of these articles, in the parallel-sided synantennomere 3 and antennal filament taken parallel to outer edge, in the maxillary article 3 along lateral surface, in the metafemur parallel to ventral edge from basal to dorsal tip. Length of metatarsomeres: measured along dorsal edge of tarsomeres, for metatarsomere 1 distance between tip of metatibia and dorsal distal edge of metatarsomere 1, for metatarsomeres 2–5 from tip of tarsomere 1 to tip of tarsomere 5. Width of metatarsomere 1: largest width in lateral view between dorsal and ventral surfaces of article, setae not taken into account. Length of ovipositor sheath: combined length of valvifer 2 and valvula 3, both measured as straight lines along ventral edge of the sclerite (Fig. 1E). Width of valvula 3 of ovipositor sheath: greatest distance between dorsal and ventral edge of valvula 3 (Fig. 1E).

Host nomenclature

The nomenclature of the taxa of Juglandaceae, which are considered as larval hosts of *Megaxyela*, follows The Plant List (2013).

Barcoding

Treatment of the specimens with DEI-GISHym numbers 5751–5752 of *Megaxyela fulvago* sp. nov., 18503–18504 of *M. pulchra* sp. nov.: for DNA extraction, the single leg of these adults was removed and submitted to the Canadian Centre for DNA Barcoding (CCDB) in Guelph, Canada, where the DNA sequencing was performed (see Blank *et al.* 2013 and Schmidt *et al.* 2017 for details). Sequencing of *M. gigantea* (2 ♀♀, 1 ♂ from 1996, 2002), *M. parki* Shinohara, 1992 (3 ♀♀ from 1990, 1993) and of additional specimens of *M. pulchra* sp. nov. (2 ♀♀ from 1994, 1998) was unsuccessful, supposedly due to the age of the pinned material, relaxing in a moist chamber before mounting, and supposedly due to storage in a collection environment where 1,4-dichlorobenzene is continuously applied for pest control. Data of the analyzed specimens are accessible through the website of Barcode of Life Data Systems (BoldSystems, http://www.boldsystems.org).

Treatment of the specimens with DEI-GISHym numbers 22355, 22513 and 22515 of *Megaxyela euchroma* sp. nov., 5237, 5239 and 30883 of *M. fulvago* sp. nov., 18507 of *M. gigantea*, 30796 of *M. langstoni*, 30767 and 30797 of *M. major*, 22347, 22349 and 86249 of *M. pulchra* sp. nov., 22354 and 22521 of *M. togashii*: total genomic DNA was extracted from one leg or from the genital capsule (without mechanical disruptions) of these specimens using the E.Z.N.A. Tissue DNA Kit (Omega Bio-tek Inc., Norcross, USA) according to the manufacturer protocol for tissue DNA, except some smaller modifications. Lysis time was at least 3 hours for the legs and 4 hours for the genital capsules. Elution was performed twice with 100 µl Elution Buffer each. A partial fragment (658 bp) of the mitochondrial cytochrome c oxidase subunit I (COI) gene was amplified by PCR using the primers SymF2 (5'-TTTCAACAAATCATAAARAYATTGG-3') and SymR2 (5'-TAAACTTCTGGRTGTCCAAARAATCA) (Prous *et al.* 2016). Amplifications were performed in 15 µl reactions containing 7.5 µl 2 × Qiagen Multiplex PCR Master Mix (Qiagen, Hilden, Germany), 0.2 µM of each primer, RNase-free water and template DNA (1–3 µl). Amplification conditions were as follows: initial PCR activation step at 95°C 5 min, 38 cycles of 30 s denaturing at 95°C, 90 s annealing at 46°C, 1 min extension at 72°C, followed by a final extension of 30 min at 68°C. PCR products were visualized on a 1.4% agarose gel stained with Gel Red (0.1, Biotium, Hayward, USA). PCR products were purified with Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase (Life Technologies, Darmstadt, Germany) and sequenced on an ABI3730XL sequencer using Big Dye v. 3.1 Terminator Kit (Thermo Fisher Scientific, Darmstadt, Germany) by Macrogen Europe (Amsterdam, the Netherlands. Sequencing was performed with the same primers used for amplification. Sequences were checked, manually edited using Geneious 9.1.2 (Kearse *et al.* 2012) and aligned using BioEdit 7.2.5 (Hall 1999).

All sequences of the *Megaxyela* species have been deposited in GenBank. The individual accession numbers are listed in Table 1. For the calculation of the cladogram we considered two specimens of *Macroxyela ferruginea* (Say, 1824) (GenBank accession numbers EF032211.1, KF936523.1) in addition.

The evolutionary history was inferred by using the Maximum Likelihood method conducted in MEGA7 (Kumar *et al.* 2016). The best-fitting model for the analysis, the Jukes-Cantor model (Jukes & Cantor 1969), was retrieved by jModelTest 2.1.7 (Darriba *et al.* 2012). It was run with 1000 bootstrap replications. Bootstrap values > 50% are shown on the ML tree next to the concerned nodes. The tree is drawn to scale, with branch lengths measured as the number of substitutions per site. The analysis involved 22 nucleotide sequences. There were a total of 658 positions in the final dataset, and all sites were used. The number of base differences per site (p-distance) between sequences was calculated. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair.

Imaging

Digital images of the specimens were taken with a Leica DFC450C camera attached to a Leica M205 C stereo microscope. Lighting was either from the high diffuse dome illumination Leica LED5000 HDI or from a cold light source attached to double light guides which produced indirect illumination by diffused light reflected from the inner surface of a styrofoam cup set up around the specimen. A grey card was used as the background and for white balance. Images from preparations of the penis valves and an ovipositor were taken from an Olympus BX50 compound microscope with a Leica DFC450 C camera. For this purpose, the specimens were mounted in glycerin temporarily. Composite images with an extended depth of field were created using the software CombineZP (Hadley 2010). Large specimens exceeding the field of view of the camera were stitched with Image Composite Editor (Microsoft Research 2015).

Table 1. COI sequences of *Megaxyela* species analyzed in this work, with specimen identifier (DEI-GISHym number), sex, collection data (including deposition of the voucher), length of COI-5P sequence (bp), and GenBank accession number.

DEI-GISHym	Sex	Collection data	bp	GenBank
		Megaxyela euchroma Blank, Shinohara & Wei sp. nov.		
22355	♀	China, Zhejiang Province, Kaishan, Laodian, Mt. Tianmushan, Lin'an, 30.333° N, 119.433° E, 1150 m alt., 16 Apr. 2014, leg. A. Shinohara, NSMT	658	KU323846
22513	♂	China, Zhejiang Province, Kaishan, Laodian, Mt. Tianmushan, Lin'an, 30.333° N, 119.433° E, 1150 m alt., 9 Apr. 2014, leg. A. Shinohara, NSMT	658	KU323847
22515	♂	China, Zhejiang Province, Kaishan, Laodian, Mt. Tianmushan, Lin'an, 30.333° N, 119.433° E, 1150 m alt., 4 Apr. 2014, leg. A. Shinohara, SDEI	658	KU323848
		Megaxyela fulvago Blank, Shinohara & Wei sp. nov.		
5237	♂	China, Hunan Province, Mt. Yunshan, nr. Wugang, 26.650° N, 110.617° E, 1250 m alt., 12 Apr. 2012, leg. A. Shinohara, NSMT	245	KX154260
5239	♂	China, Hunan Province, Mt. Yunshan, nr. Wugang, 26.650° N, 110.617° E, 1250 m alt., 12 Apr. 2012, leg. A. Shinohara, SDEI	658	KX154259
5751	♂	China, Hunan Province, Mt. Yunshan, nr. Wugang, 26.650° N, 110.617° E, 1250 m alt., 12 Apr. 2012, leg. A. Shinohara, NSMT	658	KF642802
5752	♀	China, Hunan Province, Mt. Yunshan, nr. Wugang, 26.650° N, 110.617° E, 1250 m alt., 12 Apr. 2012, leg. A. Shinohara, NSMT	658	KF642873
30882	♀	China, Zhejiang Province, Kaishan Laodian, Tianmushan, Lin'an, 30.343° N, 119.435° E, 1140 m alt., 10 Apr. 2014, leg. Liu Ting & Yu Xinjie, CSCS	658	KX922681
30883	♀	China, Zhejiang Province, Kaishan Laodian, Tianmushan, Lin'an, 30.343° N, 119.435° E, 1110 m alt., 14 Apr. 2016, leg. Li Zejian, Liu Mengmeng & Chen Zhiwei, CSCS	658	KX922682
		Megaxyela gigantea Mocsáry, 1909		
18507	♂	South Korea, Gangwon-do, Mirugam (Pugdaesa), Mt. Odaesan, 37.800° N, 128.567° E, 1300 m alt., 1 Jun. 2002, leg. A. Shinohara, NSMT	261	KU323849
		Megaxyela langstoni Ross, 1936		
30796	♀	USA, Oklahoma, Pawnee County, Pawnee, 352736 East Hwy 64, 36.292° N, 96.716°W, 9–23 Apr. 2016, leg. C. Apgar, USNM	658	KX922683
		Megaxyela major (Cresson, 1880)		
30767	♀	USA: Oklahoma, Pawnee County, Pawnee, 352736 East Hwy 64, 36.292° N, 96.716° W, 23 Apr.–3 May 2011, leg. C. Apgar, USNM	658	KX154258
30797	♀	USA: Oklahoma, Pawnee County, Pawnee, 352736 East Hwy 64, 36.292° N, 96.716° W, 9–23 Apr. 2016, leg. C. Apgar, USNM	658	KX922684
		Megaxyela pulchra Blank, Shinohara & Sundukov sp. nov.		
18503	♂	South Korea, Gangwon-do, Mirugam (Pugdaesa), Mt. Odaesan, 37.800° N, 128.567° E, 1300 m alt., 1 Jun. 2002, leg. A. Shinohara, NSMT	319	KC974015
18504	♂	China, Hubei Province, Shennongjia, Guanmenshan, 31.433° N, 110.367° E, 1580 m alt, 21 May 2010, leg. A. Shinohara, NSMT	658	KC974499
22347	♀	South Korea, Gangwon-do, Mirugam (Pugdaesa), Mt. Odaesan, 37.800° N, 128.567° E, 1300 m alt., 1 Jun. 2002, leg. A. Shinohara, NSMT	658	KU323842
22349	♀	South Korea, Gangwon-do, Mirugam (Pugdaesa), Mt. Odaesan, 37.800° N, 128.567° E, 1300 m alt., 27 May 2002, leg. A. Shinohara, NSMT	658	KU323843
86249	♀	Russia, Primorskiy Kray, Ussuri Nature Reserve, 43.644° N, 132.346° E, 150 m alt., 23 May 2016, leg. K. Kramp, M. Prous & A. Taeger, ZIN	658	KX922685
		Megaxyela togashii Shinohara, 1992		
22354	♂	Japan, Honshu, Okayama-shi, Tamagashi, 43.717° N, 133.967° E, 10 m alt., 3 May 2005, leg. A. Shinohara, NSMT	658	KU323844
22521	♂	Japan, Honshu, Okayama-shi, Tamagashi, 43.717° N, 133.967° E, 10 m alt., 2 May 2006, leg. A. Shinohara, NSMT	658	KU323845

The images were processed with PhotoImpact (Ulead Systems Inc.) and Adobe Photoshop CS4 (Adobe Systems Inc.) and mounted with CorelDraw (Corel Co.).

The distribution map was prepared from draft maps produced by Carto Fauna-Flora 1.2 (Barbier & Rasmont 1996) and was enhanced with help of Adobe Photoshop CS4.

Specimen citation

Original labels of type specimens are quoted literally between "…". Data for paratypes and additional material is listed in a standardized way. Additional explanations and interpretations, like geographic coordinates not written on the collection label, are given in square brackets […].

Collection abbreviations

AEIC = American Entomological Institute, Gainesville FL, USA (D. Wahl)
ANSP = The Academy of Natural Sciences, Dept of Entomology, Philadelphia MA, USA (D. Azuma)
CALS = College of Agriculture and Life Sciences, Seoul National University, Suwon, South Korea (K.-S. Woo)
CIS = Center for Insect Systematics, Kangwon National University, Chuncheon, South Korea (K.-T. Park)
CNC = Canadian National Collection / Agriculture Canada, Ottawa, Canada (H. Goulet)
CSCS = Key Laboratory of Cultivation and Protection for Non-Wood Forest Trees (Central South University of Forestry and Technology), Ministry of Education, Central South University of Forestry and Technology, Changsha 410004, Hunan Sheng, China (M. Wei)
CUIC = Cornell University Insect Collection, Ithaca NY, USA (E.R. Hoebeke, J.K. Liebherr)
SDEI = Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (S.M. Blank, A. Taeger)
EMEC = University of California, Essig Museum of Entomology, Berkeley CA, USA (C. Barr, W. Middlekauff)
HNHM = Hungarian Natural History Museum, Department of Zoology, Budapest, Hungary (Z. Vas, S. Csösz, L. Zombori)
IBSS = Institute of Biology and Soil Science, Vladivostok, Russia (A. Lelej)
INHS = Illinois Natural History Survey, Champaign, Illinois, USA (C. Favret, K.R. Zeiders)
IZCAS = Institute of Zoology, Chinese Academy of Sciences, Beijing, China (G. Yang)
KUEL = Kobe University, Faculty of Agriculture, Entomological Laboratory, Kobe, Japan (K. Maeto)
LSAF = Lishui Academy of Forestry, Lishui, Zhejiang, China (Z. Li)
MSUC = Michigan State University, East Lansing MI, USA (G.L. Parson, F.W. Stehr)
NHRS = Naturhistoriska riksmuseet, Sektionen for entomologi, Stockholm, Sweden (H. Vårdal, L.-Å. Janzon)
NSMT = National Museum of Nature and Science, Department of Zoology, Tsukuba, Japan (A. Shinohara)
NYSM = New York State Museum, Albany NY, USA (T.L. McCabe)
OSAC = Oregon State Arthropod Collection, Corvallis, USA (S. Fitzgerald, D. Judd)
OSU = The Ohio State University, Museum of Biological Diversity, Department of Entomology, Columbus OH, USA (A. Sharkov)
UOP = University of Osaka Prefecture, Sakai, Japan (N. Hirai)
USNM = Smithsonian Institution, National Museum of Natural History, Department of Entomology, Washington DC, USA (D.R. Smith)
YUIC = Yeungnam University, Department of Biology, Yeungnam University Insect Collections, Kyungsan, South Korea (J.-W. Lee)
ZIN = Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (S.A. Belokobylskij, A.G. Zinovjev)

Comparative material examined

Below we discuss the individual species as far as additional information has been gained since the revisions of Shinohara (1992) and Smith & Schiff (1998). We studied the following material of Nearctic species, which is not listed in detail below: *Megaxyela alisonae* D.R. Smith & Schiff, 1998: 3 ♀♀ from USA: New York (including holotype), Ohio (EMEC, NYSM, OSU); *M. aviingrata*: 9 ♀♀ from Canada: Ontario and from USA: Indiana, Mississippi, New York (including holotype) (CNC, CUIC, EMEC, INHS, MSUC, USNM); *M. bicoloripes* (Rohwer, 1924): 4 ♀♀ from USA: Mississippi (holotype), Pennsylvania, Virginia, West Virginia (AEIC, USNM); *M. tricolor* (Norton, 1862): 1 ♀, 3 ♂♂ from Canada: Ontario and from USA: Connecticut, Kansas (holotype), Illinois (INHS, USNM).

Results

Genetic analysis

The internal branching of *Megaxyela* resulting from the analysis of COI sequences of two Nearctic and five East Asian species is (*M. langstoni* + *M. major*) + (*M. euchroma* sp. nov. + (*M. fulvago* sp. nov., *M. gigantea*) + (*M. togashii* + *M. pulchra* sp. nov.)) (Fig. 2). *Megaxyela* is supported by a bootstrap value

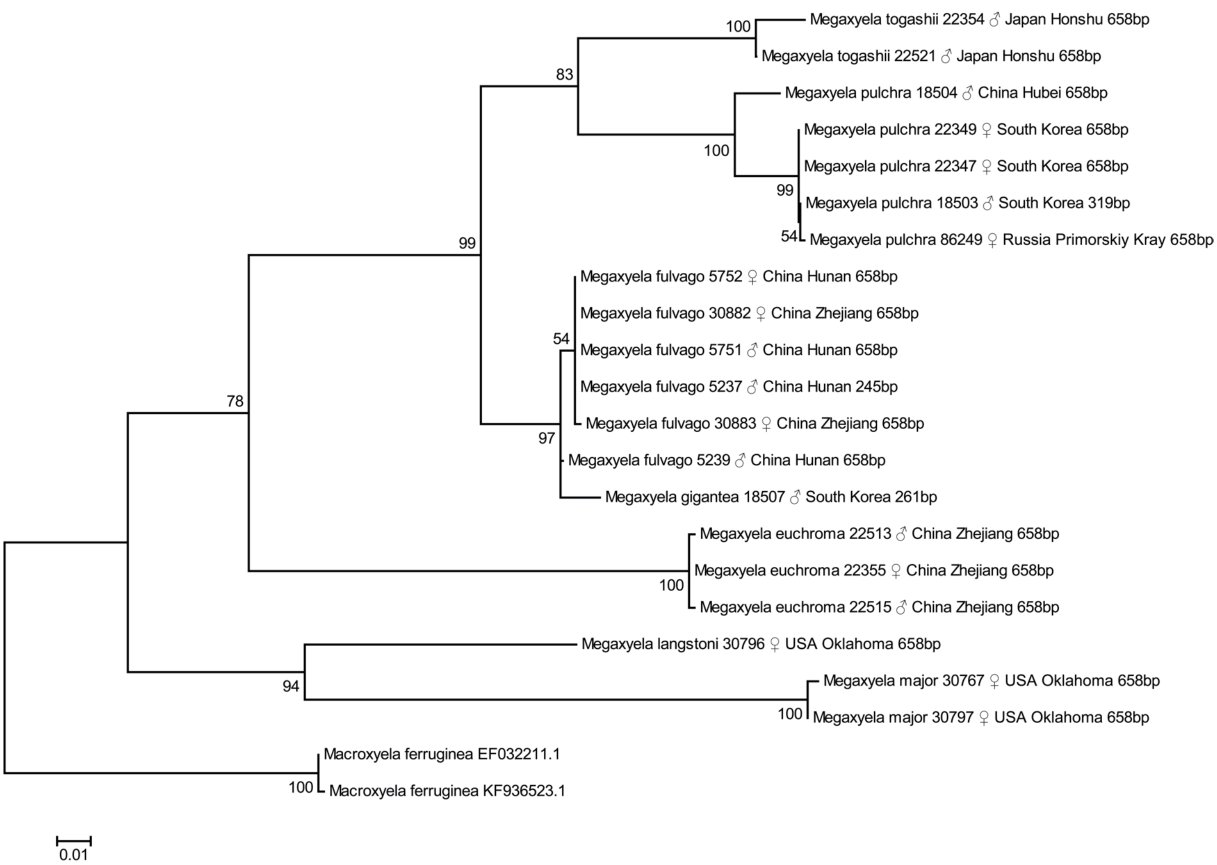

Fig. 2. Phylogenetic hypothesis of *Megaxyela* Ashmead, 1898, based on a Maximum Likelihood analysis of the barcoding region (COI-5P) applying the the Jukes-Cantor model. Two specimens of *Macroxyela ferruginea* (Say, 1824) have been included as outgroup. See Material and Methods for details. Bootstrap values above 50 % are shown next to the concerning nodes. The labels of the individual specimens consist of species name, voucher number (for *Megaxyela* identical with the DEI-GISHym numbers used in the text, for *Macroxyela* GenBank accession number), sex (♀ for females, ♂ for males) or larva, country and province of origin, and sequence length.

of 100%, the single nodes between species by 78–99%. The nearest neighbors *Macroxyela ferruginea* and *Megaxyela langstoni* are separated by a minimum pairwise distance of 13.7%. The species, for which more than one specimen could be analyzed genetically, result as monophyletic, each with a bootstrap support of 100%, except for the group of *M. fulvago* sp. nov., which also includes a specimen of *M. gigantea* (bootstrap 97%). The maximum intraspecific variation ranging from 0.3% (*M. euchroma* sp. nov., *M. major*) to 3.1% (*M. pulchra* sp. nov.) is always smaller than the minimum interspecific distance ranging from 7.6% (*M. fulvago* sp. nov. – *M. togashii*) to 13.5% (*M. langstoni – M. major*).

Taxonomical treatment

Class Hexapoda Blainville, 1816
Order Hymenoptera Linnaeus, 1758
Family Xyelidae Newman, 1834
Subfamily Macroxyelinae Ashmead, 1898

Megaxyela Ashmead, 1898

Megaxyela Ashmead in Dyar, 1898a [May]: 214 (*nec* Ashmead in Dyar 1898b [July]: 174), type species: *Xyela major* Cresson, 1880 (now *Megaxyela major*), by original designation.
Odontophyes Konow, 1899: 42, type species: *Pleroneura avingrata* Konow, 1899 (unjustified emendation and homonym of *Pleuroneura* [sic!] *aviingrata* Dyar, 1898; now *Megaxyela aviingrata*), by monotypy.
Megaloxyela Schulz, 1906: 88, unjustified emendation of *Megaxyela* Ashmead, 1898.
Paraxyela MacGillivray, 1912: 294, type species: *Xyela tricolor* Norton, 1862 (now *Megaxyela tricolor*), by original designation.

Odontophyes – Ross 1932: 161 (synonymy with *Megaxyela*).
Paraxyela – Ross 1932: 161 (synonymy with *Megaxyela*).
Megaloxyela – Smith 1978: 24 (listed in synonymy with *Megaxyela*).

Remarks

Megaxyela species differ from other extant xyelids by the following characters: carina along inner orbit present (e.g., Figs 3F–G, 4G), sometimes obscured by other surface sculpture (e.g., Figs 6C, 8F); vein Sc2 of fore wing joining R at 0.25–0.50 of distance between separation of Rs from R and pterostigma (Fig. 1A–B); hind legs extended, about 1.5–2.0 × as long as body (e.g., Fig. 3A–B, 3D–E). The taxonomic recognition of *Megaxyela* from other extant Xyelidae is possible with the keys of Ross (1937), Benson (1945) and Blank (2002).

Megaxyela bicoloripes (Rohwer, 1924)

Odontophyes bicoloripes Rohwer, 1924: 215 (♀, type locality: USA, Mississippi, Agricultural College).

Megaxyela bicoloripes – Ross 1932: 162–164 (combination). — Smith & Schiff 1998: 639–640 (key), 642 (description, distribution, references), figs 10, 14, 26–29, 34.

Material examined

USA: 1 ♀, West Virginia, Pocahontas County, Monongahela National Forest, ca 38.63° N, 79.83° W, Plot 17, lower Site, 7 May 2001, Malaise trap, L. Butler & J. Strazanac leg., DEI-GISHym 30766 (USNM).

Remarks

The above data from West Virginia represent a new state record. Among others, the species has been found in the neighboring states of Pennsylvania and Virginia (Smith & Schiff 1998).

Megaxyela euchroma Blank, Shinohara & Wei sp. nov.
urn:lsid:zoobank.org:act:63EF6069-E728-4107-8DC2-F02C9081880A
Figs 1F, 3A–3K, 11A, 12A, 13A

Megaxyela sp. 3 – Shinohara *et al.* 2017: fig. 15 (phylogenetic analysis).

Diagnosis

This species is unique upon the black head bearing narrow yellow lines along inner and outer orbits and a linear yellow spot on vertex (Fig. 3A–B, D, F–G), and the presence of ctenidia along the annuli of the ovipositor (Figs 1F, 12A). It is separated from other Eurasian species by the metallic blue shine of dark colored body parts (Fig. 3A–G), the laterally black terga 2–4 (Fig. 3A–E; only the ventral margins of the terga bear a narrow longitudinal white line ventrally, Fig. 3C, E), the almost completely black valvula 3 of the ovipositor sheath (Fig. 11A), the black hypopygium of the male (Fig. 3E), and the large and irregular teeth of the upper edge of the valviceps (Fig. 13A).

Etymology

The species name is a noun derived from ancient Greek ευ- (eu-, beautiful) and χρωμα (chroma, color).

Type material

Holotype

CHINA: ♀: “CSCS14007 [..., Chinese characters for Kaishan Laodian, Mt. Tianmushan, Linan, Zhejiang Province], E119°26′05″ N30°20′33″ 1142 m 2014.IV.8 [..., Chinese characters for the collectors Nie Haiyan & Hu Ping] $CH_3COOC_2H_5$”, [red:] “Holotype *Megaxyela euchroma* sp.n. det. SMBlank & AShinohara 2015”; “DEI-DISHym 22554” (CSCS).

Paratypes

CHINA: 2 ♀♀, same site as holotype, 4–5 Apr. 2015, Li Zejian leg. (LSAF); 1 ♀, same site as holotype, 8 Apr. 2014, Liu Ting and Yu Xingjie leg., CSCS14008 / DEI-DISHym 22555 (CSCS); 1 ♀, same site, 9 Apr. 2014, Liu Ting and Yu Xingjie leg., CSCS14010 / DEI-DISHym 22556 (CSCS); 1 ♂, same site, 10 Apr. 2014, Liu Ting and Yu Xingjie leg., CSCS14012 / DEI-DISHym 22557 (CSCS); 1 ♀, 2 ♂♂, same site as holotype, 11 Apr. 2015, Li Zejian leg., CSCS); 3 ♀♀, same site, 16 Apr. 2014, Nie Haiyan and Hu Ping leg., CSCS14026 / DEI-DISHym 22558–22560 (CSCS, SDEI, YUIC); 1 ♀, 1 ♂, same site, 16 Apr. 2014, Liu Ting and Yu Xingjie leg., CSCS14027 / DEI-DISHym 22561–22562, (CSCS); 1 ♂, same site, 1150 m, 4 Apr. 2015, A. Shinohara leg., DEI-DISHym 22515 (SDEI) (specimen used for barcoding); 1 ♀, same site, 8 Apr. 2014, A. Shinohara leg., DEI-DISHym 22512 (NSMT); 1 ♂, same site, 9 Apr. 2014, A. Shinohara leg., DEI-DISHym 22513 (NSMT) (specimen used for barcoding); 1 ♂, 1 ♀, same site, 11 Apr. 2015, A. Shinohara leg., DEI-DISHym 22514, DEI-DISHym 22516 (NSMT); 1 ♀, same site, 15 Apr. 2014, A. Shinohara leg., DEI-DISHym 22511 (NSMT); 3 ♀♀, same site, 16 Apr. 2014, A. Shinohara leg., DEI-DISHym 22509–22510 and 22355 (latter specimen used for barcoding) (NSMT, SDEI).

Description

Female

Color. Body black with white, yellow white and red brown pattern, black parts with blue tinge (Fig. 3A–B). Head black with three yellow white lines, one on vertex posterior of eye, one along dorsal half of inner

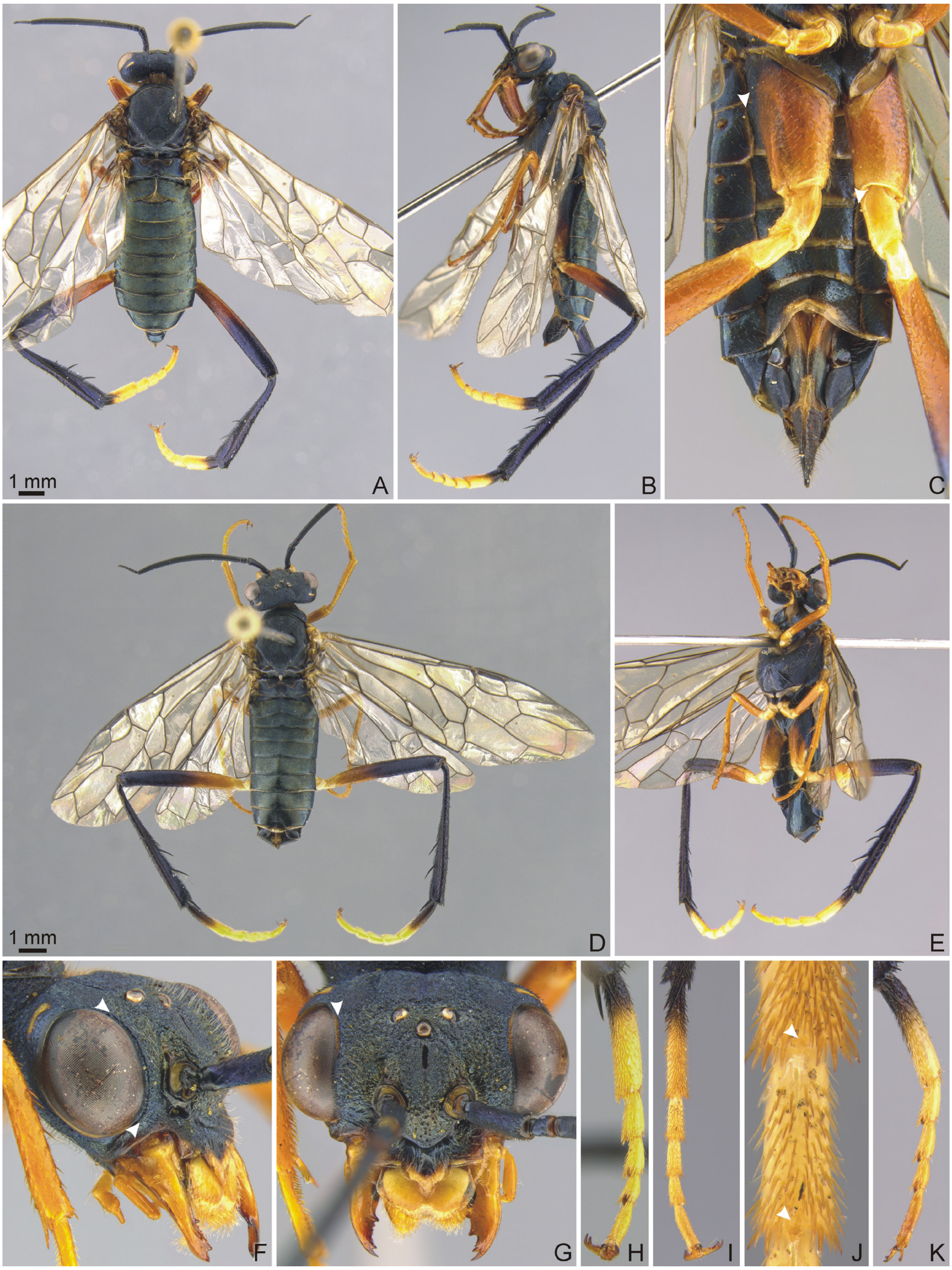

Fig. 3. *Megaxyela euchroma* Blank, Shinohara & Wei sp. nov. **A–B**. Habitus dorsal/lateral (♀, holotype, DEI-GISHym 22554, CSCS). **C**. Abdomen ventral, arrowheads indicating white stripe along ventral edge of terga (♀, 22511, NSMT). **D–E**. Habitus dorsal/lateroventral (♂, 22514, NSMT). **F–G**. Head, obliquely lateral/frontal, arrowheads indicating carina along inner orbit (♂, 22510, NSMT). **H–K**. Metatarsus, lateroventral (♀, holotype, 22554, CSCS), ventral (♀, 22510, NSMT), tarsomeres 1–2, ventral, arrowheads indicating small pulvilli (♀, 22509, NSMT), lateroventral (♂, 22513, NSMT).

orbits, one along ventral half of outer orbits and along ventral edge of eye; clypeus along anterior margin, labrum, mandibles and most of other mouthparts red brown to white (similar to Fig. 3F–G). Antenna black. Tegula, dorsolateral corner and narrow lateroventral margin of pronotum yellow white. Abdominal terga 1–8 with narrowly white distal margins, lateroventral portions of terga 2–7 with continuous 50–100 µm wide white stripe along ventral margin (Fig. 3C). Abdominal sterna 2–7 broadly white along lateral and distal margins (Fig. 3C). Valvifer 2 of ovipositor red brown in basal half, black in distal half, valvula 3 black with brown tip, membrane in between valvifer 2 and valvula 3 white (Fig. 11A). Fore and mid legs red brown, coxae predominantly black from bases, trochanters partly white. On hind leg, basal third of coxa laterally black, distal portion red brown, trochanter and trochantellus white, femur predominantly red brown in basal half, predominantly black in distal half, tibia black, tarsus white, tarsomere 1 weakly infuscate in basal third (Fig. 3A–C, H–I). Wings weakly brown stained, venation brown, pterostigma black (Fig. 3D–E), sometimes brown (Fig. 3A–B, immature specimens?).

Morphology. Body 11.3–13.1 mm, fore wing 14.1–14.6 mm long. POL : OOL : OCL = 1.0 : 1.6–1.8 : 1.8–2.0. Interantennal distance 0.9–1.0 × as wide as distance between torulus and eye margin, malar space 0.4–0.5 × as wide as interantennal distance. Eye 1.3–1.4 × as long as wide, frons at dorsal edge of antennal toruli 1.6 × as wide as maximum diameter of eye. Synantennomere 3 (4.0–)4.5–4.9 mm, filament 0.9–1.1 mm, with 7–8 articles (9 in one specimen). Article 3 of maxillary palp 0.5–0.6 mm. Ovipositor sheath 2.5–2.7 mm, valvula 3 1.4–1.6 × as long as valvifer 2, valvula 3 2.0–2.1(–2.2) × as long as wide. On hind leg, femur (4.5–)4.9–5.2 mm, tibia (5.4–)5.9–6.5 mm, tarsus (4.3–)4.6–5.2 mm, tarsomere 1 4.2–4.4 × as long as wide, longer distal spur of tibia 0.4–0.5 × as long as tarsomere 1, subapical tooth of claw stout and little shorter than apical tooth. Head dull, medial part of frons and vertex minutely areolate, lateral parts of frons rugose, gena minutely areolate (Fig. 3F and 3G). Inner orbit and ventral half of gena with carina, on inner orbit partly obscured by generally rugose structure. Mesonotum minutely areolate, posterio-medial part of medial lobes of mesoscutum and lateral parts of mesoscutellum rugulose. Mesepisternum minutely areolate, dull, with scattered 20 µm large pits. Metatarsomere 1 dorsally almost glabrous, laterally sparsely setose, lateroventrally with some stout setae up to 150 µm, ventrally densely setose, setae about 100 µm long (Fig. 3H–I). Pulvilli present on metatarsomeres 1–4, on tarsomere 1 pulvillus 70–100 µm long, on tarsomere 4 200–230 µm (Fig. 3H–J). Valvula 3 of ovipositor sheath convex dorsally and ventrally in basal and medial sections, preapically weakly concave, setae up to 250 µm long scattered mainly along dorsal and ventral margins (Fig. 11A). Ovipositor about 2.1 mm long, weakly curved ventrally, valvula 1 and valvula 2 without bulbous areas (Fig. 12A). Valvula 1 in distal 0.6 with annuli, basal annuli sigmoid, distal annuli weakly oblique, annuli with ctenidia composed of minute denticles, ventral edge in distal 0.3 bearing serrulae, cypsellae between distal 6 serrulae deep (Figs 1F, 11A). Valvula 2 in distal 0.4 with annuli, basal annuli weakly curved, distal annuli straight, annuli with ctenidia, denticles larger than those on valvula 1, dorsal edge of valvula 2 indented between annuli.

Male

Color. Similar to female (Fig. 3D–G, K). Subgenital plate and genitalia black.

Morphology. Body 9.4–10.2 mm, fore wing 11.9–12.3 mm long. POL : OOL : OCL = 1.0 : 1.5–1.8 : 1.6–1.9. Interantennal distance 0.9–1.0 × as wide as distance between torulus and eye margin, malar space 0.4–0.5 × as wide as interantennal distance. Eye 1.3–1.4 × as long as wide, frons at dorsal edge of antennal toruli 1.6–1.7 × as wide as maximum diameter of eye. Synantennomere 3 4.0–4.4 mm, filament (0.8–)0.9–1.1 mm, with 7–8 articles. Article 3 of maxillary palp 0.5 mm long. On hind leg, femur 4.1–4.4 mm, tibia 5.1–5.3 mm, tarsus 4.2–4.5 mm, tarsomere 1 4.7–5.3 × as long as wide, longer distal spur of tibia 0.40 × as long as tarsomere 1. Claws and microsculpture similar to female. Setation of metatarsus less dense than in female (Fig. 3K). Subgenital plate bluntly pointed at apex. Valviceps of penis valve distally evenly rounded, basal 0.4 of upper side expanded to a roundly angular lobe, upper edge of valviceps distal of lobe weakly concave, with large, irregular teeth. Distal half of valviceps in upper and medial portion with long setae, distal of middle in lower portion with dense assemblage of short, conical setae (Fig. 13A).

Remarks

Megaxyela euchroma sp. nov. is characterized by a number of unique characters (see Diagnosis). All other East Asian species are completely white on the ventral portion and partly on the dorsolateral portion of terga 2–3 or 2–4. In these cases, the white band on terga 2–3 or 2–4 is much wider than on the subsequent terga. The head is more extensively yellow or red brown, at least on the gena in *M. gigantea*, *M. pulchra* sp. nov. and *M. togashii*, or the eye is completely surrounded by black except for the malar space in *M. parki*. *Megaxyela euchroma* sp. nov. and *M. parki* share the white metatarsus, which is black in the other East Asian species.

With respect to the white pattern of the terga, *M. euchroma* sp. nov. is similar to the North American *M. alisonae*, *M. bicoloripes*, *M. inversa* sp. nov. and *M. tricolor* (Smith & Schiff 1998). *Megaxyela alisonae* and *M. bicoloripes* have a white metatarsus similar to *M. euchroma* sp. nov., while *M. tricolor* has a black metatarsus. In the Nearctic species, a yellow white pattern on the orbits and the vertex, similar to that of *M. euchroma* sp. nov., is absent. *Megaxyela alisonae* and *M. bicoloripes* bear an extensive red brown pattern on thorax and abdomen, which is absent in *M. euchroma* sp. nov. *Megaxyela inversa* sp. nov. differs in the shape of the ovipositor sheath, which is straight dorsally in the basal and the medial sections, vs convex in *M. euchroma* sp. nov.

The analysis of the COI sequences supports the monophyly of the studied specimens by a bootstrap of 100%. The maximum intraspecific variation is 0.3%. The nearest neighbor, *M. fulvago* sp. nov., is placed at a distance of 12.7% (Fig. 2).

All the available adults were found on the undergrowth of open forests during cloudy weather. There were *Juglans* trees nearby and new shoots of leaflets were beginning to grow.

Megaxyela fulvago Blank, Shinohara & Wei sp. nov.

urn:lsid:zoobank.org:act:DF04584F-B33D-42A7-836D-E758A66F4081

Figs 4A–G, 11B, 12B–C, 13B

Megaxyela gigantea – Takeuchi 1940: 484 (misidentification). — Maa 1949: 30 (misidentification).
Megaxyela sp. 2 – Shinohara *et al.* 2017: fig. 15 (phylogenetic analysis). — Blank *et al*. 2017: 115.

Diagnosis

The red brown head, prothorax and mesothorax are unique to this species.

Etymology

The Latin noun *fulvago* indicates the predominantly pale brown color of this species.

Type material

Holotype

CHINA: ♂: "[CHINA: Hunan] Mt. Yunshan 1250 m [alt.] 26°39′ N, 110°37′ E nr. Wugang 12.IV.2012 [leg.] A. Shinohara"; "DEI-GISHym 5236"; [red:] "Holotype *Megaxyela fulvago* det. SMBlank & AShinohara 2015" (CSCS).

Paratypes (6 ♀♀, 6 ♂♂)
CHINA: 1 ♀, 5 ♂♂, same collecting data as holotype, DEI-GISHym 5235, 5237–5239, 5751–5752 (5237, 5239, 5751–5752 used for barcoding) (SDEI, NSMT); 1 ♀, Jiangsu Sheng, Nanjing, 32.06° N, 118.78° E, 1 May 1985, Jinniang leg. (CSCS); 2 ♀♀, 1 ♂, Jiangsu Sheng ["Prov. Kiangsu"], Zhenjiang ["Chinkiang"], 32.20° N, 119.43° E, 24 Apr.–1 May 1918 (IZCAS) (Takeuchi 1940; Maa 1949; images for re-identification provided by Yang Ganyan); 1 ♀, Zhejiang Province, Kaishan Laodian, Tianmushan, Lin'an, 30.343° N, 119.435° E, 1140 m alt., 10 Apr. 2014, Liu Ting and Yu Xinjie leg., CSCS14012, DEI-GISHym 30882 (specimen used for barcoding) (CSCS); 1 ♀, same locality, 1110 m alt., 14 Apr. 2016, Li Zejian, Liu Mengmeng and Chen Zhiwei leg., CSCS16143, DEI-GISHym 30883 (specimen used for barcoding) (CSCS).

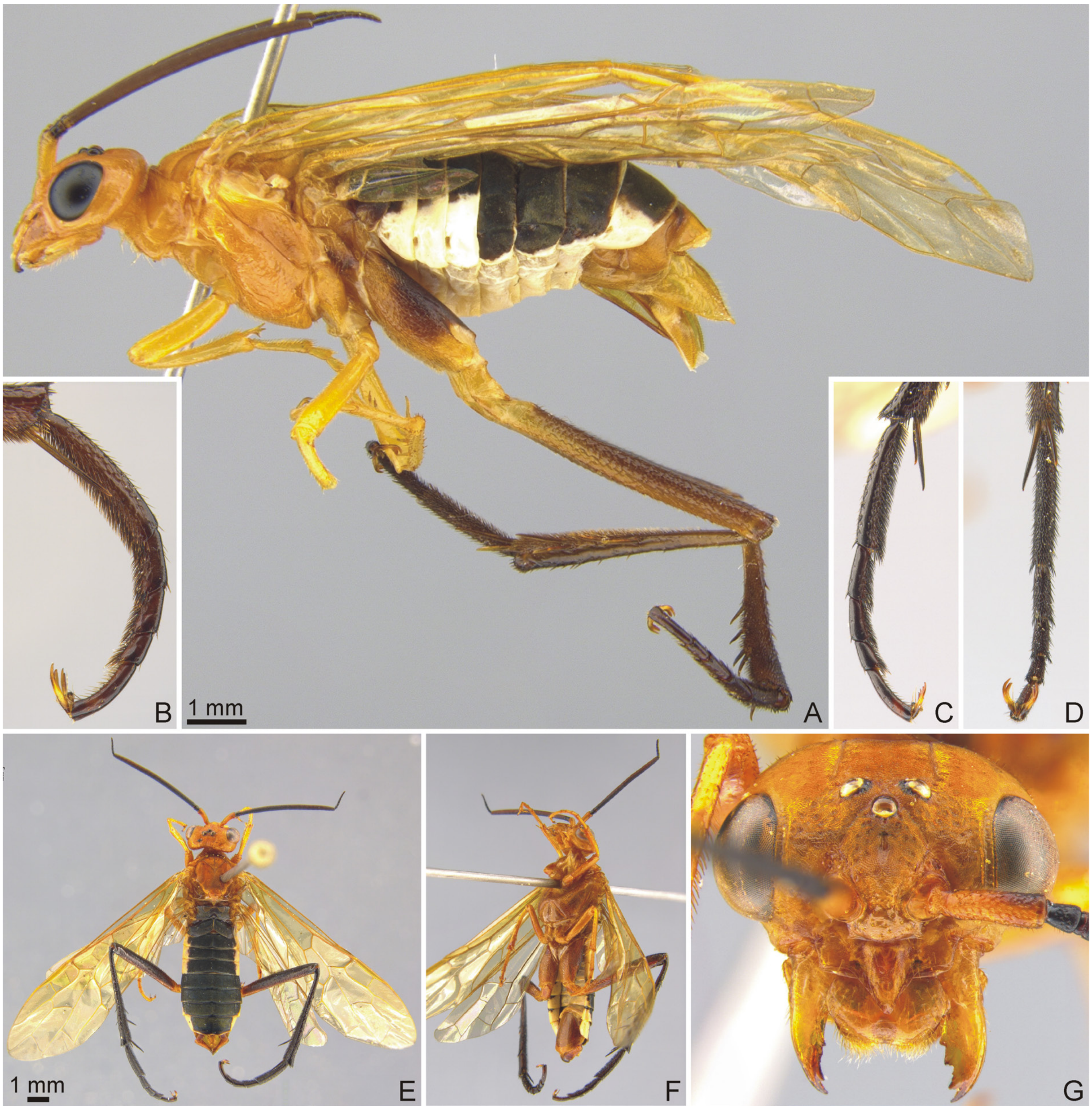

Fig. 4. *Megaxyela fulvago* Blank, Shinohara & Wei sp. nov. **A**. Habitus lateral (♀, DEI-GISHym 5752, NSMT). **B**. Metatarsus lateral (♀, 5752, NSMT). **C–D**. Metatarsus lateral/ventral (♂, holotype, 5236, CSCS). **E–F**. Habitus dorsal/lateroventral (♂, holotype, 5236, CSCS). **G**. Head frontal (♂, 5239, NSMT).

Description

Female

Color. Body red brown with black-and-white pattern, black parts partly with bronze tinge (Fig. 4A). Head and thorax red brown (specimen 30882 with diffuse transverse stripe on vertex – artifact?), posterior half of metanotum and ventral half of metepisternum infuscate. Scape red brown, pedicel black, flagellum dark brown. Abdomen in dorsal view black with continuous white bands laterally on terga 2–4, each 0.15–0.20 × as wide as tergal width, tergum 8 with narrower lateral white band, ventral portions of terga 2–4 and 8 completely white, terga 5–6 narrowly and tergum 7 broadly white along ventral margin, terga 9+10 brown with small dark spot dorsolaterally. Sterna white. Valvifer 2 and valvula 3 red brown, membrane between valvifer 2 and valvula 3 pale (Fig. 11B). Fore and mid legs pale red brown. On hind leg, coxa red brown, infuscated laterally in middle and dorsally, trochanter and trochantellus pale red brown, femur brown dorsally and red brown ventrally, tibia and tarsus brown. Wings weakly yellow stained, venation and pterostigma yellow brown.

Morphology. Body 11.4–13.0 mm, fore wing 14.9–15.4 mm long. POL : OOL : OCL = 1.0 : 2.2–2.4 : 2.2–2.3. Interantennal distance 1.0–1.1 × as wide as distance between torulus and eye margin, malar space 0.4–0.5 × as wide as interantennal distance. Eye 1.3–1.4 × as long as wide, frons at dorsal edge of antennal toruli 1.7–1.8 × as wide as maximum diameter of eye. Synantennomere 3 4.5–4.9 mm, filament 1.1 mm, with 8–9 articles. Article 3 of maxillary palp 0.5–0.6 mm long. Ovipositor sheath 3.30–3.50 mm long, valvula 3 1.9–2.3 × as long as wide. On hind leg, femur 4.9–5.0 mm, tibia 5.6–6.0 mm, tarsus 4.1–4.3 mm, tarsomere 1 4.5–5.1 × as long as wide, longer distal spur of tibia 0.70 × as long as tarsomere 1, subapical tooth of claw stout and little shorter than apical tooth (Fig. 4B; similar to Shinohara 1992: fig. 4D). Face and vertex with areolate surface microsculpture, dull, interantennal area and frons above antennal toruli with scattered, shallow, 50 µm large pits (similar to Fig. 4G), gena weakly coriarious, shining. Mesoscutum and mesoscutellum homogeneously areolate. Mesepisternum weakly coriarious and shining, with scattered pits. Metatarsomere 1 dorsally and dorsolaterally very sparsely setose, ventrally and ventrolaterally densely setose, setae 150–200 µm long ventrally (Fig. 4B). Pulvilli absent on article 1 of metatarsus, present on articles 3–4, presence ambiguous for article 2, on article 4 pulvillus 50 µm long. Basal and medial sections of valvula 3 of ovipositor sheath convex dorsally, almost straight ventrally, preapical section concave on dorsal and ventral edge, medial to preapical section of dorsal margin with setae up to 200 µm long, ventral margin with setae up to 100 µm long (Fig. 11B). Ovipositor about 2.4 mm long, weakly curved ventrally, valvula 1 and valvula 2 with bulbous areas in middle, without ctenidia (Fig. 12B–C). Valvula 1 in distal 0.7 with very narrowly spaced, subparallel, straight, vertical annuli, ventral margin in distal 0.3 bearing small serrulae. Valvula 2 in distal 0.6 with narrowly spaced annuli, distal 0.3 of dorsal edge of valvula 1 with small denticles.

Male

Color. Similar to female (Fig. 4E–G). Metepimeron red brown or predominantly infuscate. Ventral portions of terga 5–7 predominantly white. Subgenital plate and genitalia red brown. On hind leg, coxa sometimes completely black laterally, trochanter and trochantellus red brown, femur black dorsally and medially, dark red brown ventrally and laterally, tibia and tarsus black (Fig. 4C–D).

Morphology. Body 8.8–10.7 mm, fore wing 11.3–12.8 mm long. POL : OOL : OCL = 1.0 : 1.6–1.7(–1.9) : 1.7–1.9(–2.0). Interantennal distance 0.9–1.1 × as long as distance between torulus and eye margin, malar space 0.5 × as wide as interantennal distance. Eye 1.3–1.4 × as long as wide, frons at dorsal edge of antennal toruli 1.6–1.8 × as wide as maximum diameter of eye. Synantennomere 3 (3.6–)4.0–4.6 mm, filament 1.0–1.1 mm and with 8–9 articles (one male with left filament 0.8 mm long, 6 articles, right filament 1.0 mm long, 8 articles). Article 3 of maxillary palp 0.4–0.5 µm long. On hind leg, femur 3.7–4.2 mm, tibia 4.5–5.2 mm, tarsus (3.8–)4.1–4.4 mm, tarsomere 1 4.9–5.5 × as long as wide, longer distal spur of tibia 0.60 × as long as tarsomere 1. Claws and microsculpture similar to female (Fig. 4D).

Subgenital plate bluntly pointed at apex. Valviceps of penis valve distally parabolically rounded, basal 0.3 of upper side expanded to a round lobe coiled laterally, medial 0.3–0.8 of upper edge shallowly convex, with numerous small teeth. Distal 0.7 of valviceps with long setae, most dense in medial lower portion of valviceps (Fig. 13B).

Remarks

Megaxyela fulvago sp. nov. is most similar to *M. gigantea* regarding color and structure. In both species, terga 2–4 are extensively white on the dorsolateral and ventral portion. This pattern is absent in *M. euchroma* sp. nov. and in most of the Nearctic species. White is present on the dorsal side of only terga 2–3 in *M. parki*, *M. pulchra* sp. nov. and *M. togashii*, as well as in the Nearctic *M. major*. *Megaxyela fulvago* sp. nov. and *M. gigantea* share the dull, minutely areolate and shallowly pitted face. A rugose surface structure is absent from the frons, which has been observed in the other East Asian species. *Megaxyela fulvago* sp. nov. and *M. gigantea* are primarily discriminated by color: head, prothorax and mesothorax are completely red brown in *M. fulvago* sp. nov., but these parts bear an extensive dark brown to black pattern in *M. gigantea*. The antennal filament of females is longer in *M. fulvago* sp. nov. (1.1 mm) than in *M. gigantea* (0.8 mm), and sometimes it is subdivided into fewer articles in *M. fulvago* sp. nov. (♀: 8–9; ♂: usually 8–9) than in *M. gigantea* (♀: 9; ♂: 9–10). The relative distance of POL : OOL : OCL differs weakly in males (1.0 : 1.6–1.7[–1.9] : 1.7–1.9[–2.0] and 1.0 : 1.8–2.0 : 2.0–2.2, respectively). The metatarsomere 1 of males is 4.9–5.5 × as long as wide in *M. fulvago* sp. nov. but 4.6–5.0 × in *M. gigantea*. The female of *M. fulvago* sp. nov. falls into the range of variability of *M. gigantea* regarding these two characters.

The COI sequences group the specimens identified as *M. fulvago* sp. nov. by morphology into a clade which is supported by a bootstrap of 97%. This clade additionally includes a specimen of *M. gigantea*. Supposedly this placement is an artefact caused by the short sequence length (261 bp) of this specimen. The maximum intraspecific variation within *M. fulvago* sp. nov. is 0.8%. *Megaxyela togashii* is placed at a minimum pairwise distance of 7.6% (Fig. 2).

The specimens from Mount Yunshan were collected on a sunny day flying around birch trees with lots of catkins shedding pollen. Pollen feeding of adults is well known for *Xyela* species, which bear distally modified and usually extended maxillary palps (Burdick 1961). A similar behavior is unknown for adult Macroxyelinae. Although *M. major* has been caught from catkins of willow (Bridwell 1906) and pollen has been identified from the intestine of two fossil Macroxyelinae species (Krasilov & Rasnitsyn 1982), *Megaxyela* is not specialized in pollen feeding but is facultatively palynivorous, because the labio-maxillar complex exhibits no particular modifications for the uptake of pollen as in Xyelinae.

Takeuchi (1940) and Maa (1949) referred to the specimens of *M. gigantea* collected in “Chinkiang [= Zhenjiang], Prov. Kiangsu [= Jangsu Sheng]” deposited in the collection of the Musée Heude, Shanghai at that time. Major parts of this collection have been incorporated into IZCAS, Beijing (Yang Ganyan, personal communication). The two females and one male collected in “Chinkiang” in 1918 could be identified as *M. fulvago* sp. nov. with help of photos kindly provided by Yang Ganyan. An additional female from “Chinkian” (3 May 1936, E. Suenson leg.), which we identified as *M. gigantea* prior to the recognition of *M. fulvago* sp. nov., is kept at INHS.

Megaxyela gigantea Mocsáry, 1909
Figs 5A–H, 11C, 12E, 13C, G–H

Megaxyela gigantea Mocsáry, 1909: 39 (♀, type locality: Russia, Khabarovskiy Kray, Kazakevichevo).
Megaxyela mikado Sato, 1930: 4–5, figs a–b (♀, type locality: South Korea, Suwon, Kazan).

Megaxyela mikado – Takeuchi 1937: 25 (synonymy with *M. gigantea*).
Megaxyela gigantea – Shinohara 1992: 785–789 (description, distribution, hosts, references), 794–795 (key), figs 1A–B, 2A–B, 2E, 3A–C, 4A, 4F–G.

Type material

Lectotype (here designated)

RUSSIA: ♀, lectotype of *Megaxyela gigantea*, "Ussuri Kasakewitsh [= Khabarovskiy Kray, Kazakevichevo, 48.27° N, 134.77° E] 1907 Korb"; "*Megaxyela gigantea* det. Mocsáry"; [rectangular red label without inscription]; "*Megaxyela gigantea* Mocs."; [red:] "Lectotype *Megaxyela gigantea* Mocsáry, 1909 Det. A. Shinohara 1997", in perfect condition (HNHM). The lectotype corresponds well with Shinohara's (1992) characterization of the species.

Fig. 5. *Megaxyela gigantea* Mocsáry, 1909. **A–B**. Habitus dorsal/lateroventral (♀, holotype of *M. mikado*, DEI-GISHym 22350, NSMT). **C–D**. Habitus dorsal/lateroventral (♂, 18507, NSMT). **E**. Head frontal (♀, holotype of *M. mikado*, 22350, NSMT). **F–G**. Metatarsus lateral/ventral (♀, holotype of *M. mikado*, 22350, NSMT). **H**. Metatarsus ventral (♂, 18507, NSMT).

Paralectotypes

RUSSIA: 1 ♀, same collecting data as lectotype (HNHM), Mocsáry (1909) described *M. gigantea* from an unknown number of females.

SOUTH KOREA: 1 ♀, holotype of *Megaxyela mikado*, "Suigen [= Suwon, 37.28° N, 127.02° E], Chosen [= Korea], Apr. 24., 1927, coll. K. Sato"; "270", "Type of *Megaxyela mikado* Sato", "*Megaxyela gigantea* Mocs. det. K. Sato, XI–1957", "DEI-GISHym 22350", left wings missing (NSMT). The holotype of *M. mikado* is a comparatively dark female of *M. gigantea* with a large dark brown spot on ocellar area and vertex. Terga 2–4 bear white stripes laterally, which are of equal width (see figure in Sato 1930; Shinohara & Smith 1979: fig. 13, in synonymy with *M. gigantea*). The synonymy first proposed by Takeuchi (1937) is here confirmed.

Additional material examined or reported in literature

NORTH KOREA: 1 ♀, P'yŏngan-pukto ["Pyongah Prov. N"], Mt. Myohyang, 40.02° N, 126.33° E, 23 May 1985, Vojnits & Zombori leg. (HNHM).

RUSSIA: 1 ♀, Primorskiy Kray, Voroshilovskiy rayon, southern slopes of Sikhote Alin, on river Suputinka ["Fluß Suputinka, S. Abhänge von Sichota-Alin"], 43.77° N, 131.90° E, 20 Jun. 1937, T. Samoylov leg. (NHRS).

SOUTH KOREA: 4 ♀♀, 51 ♂♂ (including DEI-GISHym 708), Chollanam-do, Mt. Nogodan, Mts. Chirisan, 35.30° N, 127.53° E, 1220 m alt., 4–5 Jun. 1996, A. Shinohara leg. (NSMT); 1 ♀, Kangwon-do, Mirugam (Pugdaesa), Mt. Odaesan, 37.80° N, 128.57° E, 1300 m alt., 30 May 1991, A. Shinohara leg. (NSMT) (Shinohara 1992); 1 ♀, same locality, 27 May 1998, A. Shinohara leg. (NSMT); 1 ♂ (specimen DEI-GISHym 18507 used for barcoding), same locality, collected from *Juglans* ?*mandshurica*, 1 Jun. 2002, A. Shinohara leg. (NSMT); 5 ♀♀, 5 ♂♂, Kyonggi-do, Suwon ["Suigen"], 37.283° N, 127.017° E, 12 May 1932, S. Fujii leg. (CIS, NSMT, USNM) (Shinohara 1992); 2 ♀♀, 4 ♂♂, same locality, 14 May 1932, S. Fujii leg. (NSMT, USNM) (Shinohara 1992); 5 ♀♀, Seoul ["Keijo"], 37.57° N, 127.00° E, 11 May 1935, K. Sato leg. (NSMT) (Shinohara 1992); 2 ♀♀, Seoul, Ch'ongnyangni ["Seiryori"], 37.58° N, 127.05° E, 6 May 1934, H. Doi leg. (UOP) (Shinohara 1992).

Description

See Shinohara (1992) and Figs 5A–B, E, 11C (ovipositor sheath).

Female

Ovipositor about 2.7 mm long, weakly curved ventrally, valvula 1 and valvula 2 bulbous distal of middle, without ctenidia (Fig. 12E). Pulvilli absent on article 1 of metatarsus, present on article 4 and 50 µm long, presence ambiguous for articles 2–3 (Fig. 5F–G).

Male

See Figs 5C–D, H, 13G–H. Valviceps of penis valve distally parabolically rounded, basal quarter of upper side expanded to a round lobe coiled laterally, medial 0.3–0.8 of upper edge with one or two shallow elevations and numerous small teeth. Distal 0.7 of valviceps with long setae, most dense in medial lower portion (Fig. 13C).

Host plant

Saito (1941), Ko (1969) and Xiao (2006) reported *Juglans ailanthifolia* Carrière (cited as *J. sieboldiana* Maxim.), *J. mandshurica* Maxim., *J. regia* L. (including the synonym *J. sinensis* [C. DC.] Dode), *Pterocarya rhoifolia* Sieb. & Zucc., and *P. stenoptera* C. DC. All recorded hostplant associations of *M. gigantea* need confirmation, because they can also refer to the new species *M. pulchra* sp. nov.

In South Korea, A. Shinohara captured a male of *M. gigantea* together with 3 ♀♀, 2 ♂♂ *M. pulchra* sp. nov. from the same *J. ?mandshurica* tree at end of May and beginning of June 2002.

Remarks

Megaxyela gigantea is similar to species with the terga 2–3 or 2–4 laterally extensively white (dorsally black in *M. euchroma* sp. nov. and in the Nearctic species except for *M. major*). It is unique among the East Asian species in the predominantly red brown head (predominantly black in *M. parki*, pale yellow color and less extensive in *M. togashii*) bearing a large infuscate spot on face and vertex (completely red brown in *M. fulvago* sp. nov.), which does not extend to the antennal toruli ventrally (spot extending to toruli in *M. pulchra* sp. nov.). As in *M. fulvago* sp. nov., the surface of the face is minutely areolate and bears scattered, shallow, 50 µm large pits (face rugose in other East Asian species at least laterally). The dorsal side of terga 2–4 is white laterally for 0.15–0.20 × the tergal width in *M. gigantea* and *M. fulvago* sp. nov., whereas the white marks are generally narrower in *M. parki* or narrower at least on tergum 4 in *M. pulchra* sp. nov. and *M. togashii*.

The single specimen studied genetically is placed within the group, which otherwise comprises *M. fulvago* sp. nov., but we interpret this placement as an artefact caused by the very short sequence length of *M. gigantea*. Morphological results indicate two separate species.

Megaxyela inversa Blank & D.R. Smith sp. nov.

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Figs 6A–G, 11D, 12D

Diagnosis

This species is unique by the very long ovipositor sheath with the dorsal outline of valvula 3 straight and the ventral outline convex, and the ovipositor curved dorsally along its longitudinal axis.

Etymology

The Latin adjective *inversus* (fem. *inversa*) indicates the shape of the ovipositor, that, in contrast to other *Megaxyela* species, is dorsally curved.

Type material

Holotype

USA: ♀: "USA West Virginia, Randolph Co., Job, 38.8528 N, 79.5293 W, 1-20 April 2012, J. Whitaker 10067, USGS-DRO 292937", [red:] "Holotype *Megaxyela inversa* det. S.M. Blank & D.R. Smith 2017", "DEI-GISHym 32152" (USNM).

Paratype

UNKNOWN: 1 ♀ , "4/22/91" [supposed collection date: 22. Apr. 1891, no collecting locality given, see insertion in Fig. 6A for original labels], DEI-GISHym 22356 (USNM).

Description

Female

Color. Black with white pattern, black parts with bronze to blue tinge (Fig. 6A, C). Head below toruli brown, clypeus and labrum white, preapical region of labrum and mandibles brown white, labial palpomeres 1–2 white (Fig. 6C). Antenna black with basal ¾ of scape in inner surface light orange. Pronotum and metanotum with bronze tinge, mesonotum and mesepisternum with blue tinge. Tegula basally brown, distally white. Abdominal terga and sterna black, terga 1–8 and sterna with white distal margins, ventral part of terga laterally with 100 µm wide white stripe, sterna 5–7 with 40–50 µm

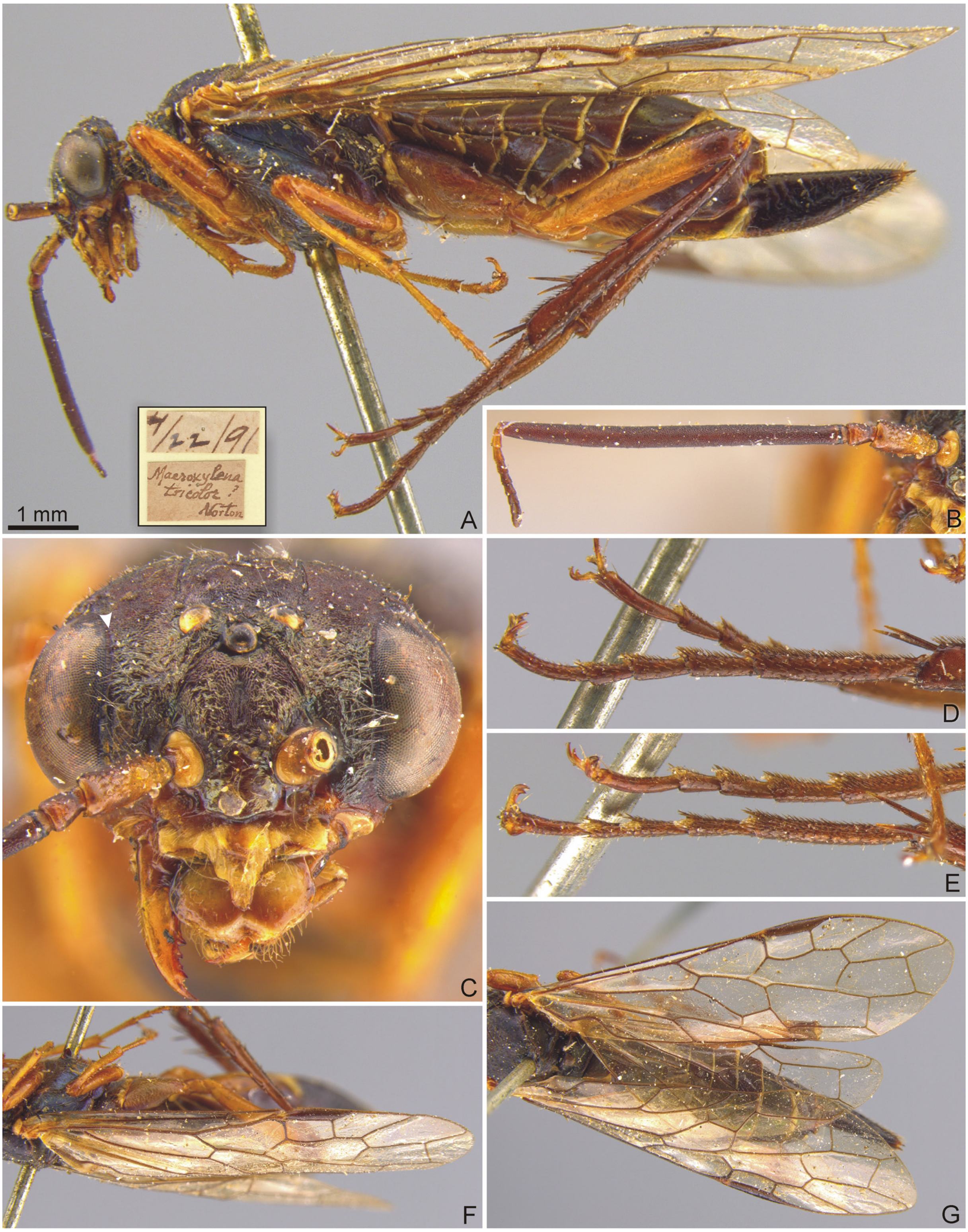

Fig. 6. *Megaxyela inversa* Blank & D.R. Smith sp. nov. (♀, paratype, DEI-GISHym 22356, USNM). **A**. Habitus, lateral; small insertion: original collection labels. **B**. Antenna. **C**. Head, frontal, arrowhead indicating carina along inner orbit. **D–E**. Metatarsus, lateral/lateroventral view. **F–G**. Wings.

wide lateral white stripe (Fig. 6A). Valvifer 2 red brown, valvula 3 black except for narrow brown tip, membrane between valvifer 2 and valvula 3 white (Fig. 11D). Legs orange, procoxa and mesocoxa basally infuscate, distal 0.20 of metafemur, complete metatibia and metatarsus black. Wing subhyaline, venation and pterostigma black (Fig. 6F–G).

Morphology. Body 10.2 mm, fore wing 11.2 mm long. POL : OOL : OCL = 1.0 : 1.3 : 1.5. Interantennal distance 1.3 × as wide as distance between torulus and eye margin, malar space 0.4 × as wide as interantennal distance. Eye 1.5 × as long as wide, frons at dorsal edge of antennal toruli 1.4 × as wide as maximum diameter of eye. Synantennomere 3 3.1 mm, filament 0.9 mm, with 9 articles. Article 3 of maxillary palp 0.4 µm. Ovipositor sheath 5.1 mm, 3.8 × as long as metatarsomere 1, valvula 3 1.3 × as long as valvifer 2, valvula 3 3.3 × as long as wide. On hind leg, femur 3.1 mm, tibia 4.5 mm, tarsus 3.6 mm, tarsomere 1 5.8 × as long as wide, longer distal spur of tibia 0.3 × as long as tarsomere 1, claws cleft, subapical tooth of claw little smaller at base than apical tooth. Head dull, lateral part of frons rugose, medial part minutely areolate with some 50 µm large pits, vertex and postocellar area mostly minutely areolate to rugulose, gena rugulose (Fig. 6C). Mesoscutum and mesoscutellum homogeneously minutely areolate. Mesepisternum medially coriarious and shining, with 20 µm large pits. Metatarsomere 1 dorsally and laterally almost glabrous, ventrally densely setose, setae 70–100 µm long (Fig. 6D). Pulvilli present on metatarsomeres 1–4, on article 1 pulvillus 150 µm long, on article 4 230 µm (Fig. 6E). Basal and medial sections of valvula 3 of ovipositor sheath straight dorsally, convex ventrally, preapical section almost straight on dorsal and ventral edge, with dense pattern of up to 200 µm long setae (Figs 6A, 11D). Ovipositor 4.6 mm long, weakly curved dorsally, without bulbous areas in middle, without ctenidia (Fig. 12D). Valvula 1 in distal 0.6 with annuli, basal annuli much more widely spaced then medial and distal annuli, medial annuli very narrowly spaced, subparallel, straight, vertical, ventral edge in distal 0.2 bearing small serrulae. Valvula 2 in distal 0.3 with widely spaced annuli, annuli not extending to ventral edge of valvula, distal 0.3 of dorsal edge of valvula 1 with partly prominent, rounded denticles.

Male

Unknown.

Remarks

The ovipositor is curved dorsally in *Megaxyela inversa* sp. nov. (Fig. 12D), which is an unusual condition in sawflies and unique in Macroxyelinae (Fig. 12A–B, E–H; Smith & Schiff 1998: figs 16–21). The predominant number of sawflies and woodwasps have the ovipositor curved ventrally or the ovipositor is straight (see, e.g., figures in Weltz & Vilhelmsen 2014). Among Xyelidae, the sheath is curved dorsally to a various degree in species of *Pleroneura* Konow, 1897 (e.g., Smith *et al.* 1977; Shinohara 1995, 2016) and in *Xyela concava* Burdick, 1961 (Burdick 1961).

Among Nearctic *Megaxyela* this species is most similar to *M. bicoloripes* and *M. tricolor* by the slender metatarsus and the red brown metafemur bearing an extensively infuscate apex. It is readily distinguished from all other *Megaxyela* species by the outline of the basal and medial portion of valvula 3, which in lateral view is straight dorsally and evenly curved ventrally. The remaining *Megaxyela* species have either both the dorsal and the ventral outlines of valvula 3 curved, or the dorsal outline is curved and the ventral straight (Fig. 11A–C, 11E–H; Smith & Schiff 1998: figs 7–11).

The paratype is presumably from North America because of its discovery in a US collection and the holotype is from West Virginia. Morphometry and figures are from the paratype since the specimen used as holotype was discovered too late to include in this paper.

Megaxyela langstoni Ross, 1936 sp. rev.
Figs 7A–F, 11E

Megaxyela langstoni Ross, 1936: 131–132 (♀♂, type locality: USA, Mississippi, Starkville, Mississippi State University).

Megaxyela langstoni – Smith 1978: 25 (listed in synonymy with *M. major*). — Smith 1979: 10 (synonymized with *M. major*).
Megaxyela major – Smith & Schiff 1998: 644–648 (misidentification, *partim*). — Ree 2012: [1] (damage to pecan). — Ree 2014: [2] (damage to pecan). — Ree 2016: [2] (damage to pecan).

Type material

Holotype

USA: ♀: "State College Miss. 4/7/32"; "J. M. Langston Collector"; "Pecan 283813"; [red:] "Holotype *Megaxyela langstoni* Ross ♀"; "INHS Type #1071"; "DEI-GISHym 30821" (INHS), left posterior leg missing. The locality data correspond with the present-day Mississippi State University of Agriculture and Applied Science in Starkville.

Additional material examined

USA: 1 ♀, Mississippi, Starkville ["Ag. Coll. Miss."], 10 Apr. 1915, C.C. Greer leg., DEI-GISHym 30822 (USNM); 1 ♀, Oklahoma, Pawnee County, Pawnee, 352736 East Hwy 64, 36.292° N, 96.716° W, Malaise trap, 9–23 Apr. 2016, C. Apgar leg., DEI-GISHym 30796 (specimen used for barcoding) (USNM); 1 ♀, 1 ♂, Texas (USNM).

Supplementary description

Female

Synantennomere 3 3.8 mm, filament 0.8 mm, with (6–)8–9 articles. Pulvilli present on metatarsomeres 1–4, on article 1 pulvillus 100 µm long, on article 4 170 µm (Fig. 7D–E). See key for additional characters.

Host plant

Pecan (*Carya illinoinensis*; cited as "*Carya pecan* A. & G." by Ross 1936) and possibly additional species of *Carya* (Dyar 1898b as *M. major*; Yuasa 1923 as *Megaxyela* sp. 1). Supposedly also the photo by Ree (2014) of gregarious larvae of *M.* '*major*' feeding on pecan refers here.

Remarks

Smith (1978, 1979) treated *Megaxyela langstoni* as a synonym of *M. major*. With some reservation, Smith & Schiff (1998) discussed differences in behavior, color and morphology as possible intraspecific variation. Here we reinstate *M. langstoni* sp. rev. as a valid species. The analysis of the barcoding region of three females, all originating from a collection site in Oklahoma, resulted in two clades (DEI-GISHym 30796 and 30767 + 30797, respectively) separated by a minimum pairwise distance of 13.5%, while the two specimens included in the clade 30767 + 30797 are separated by a mimimum pairwise distance of only 0.3% (Fig. 2). This observation is paralleled by different coloration of the adults corresponding with the type material and the descriptions of *M. langstoni* and *M. major*: Specimen 30796 agrees with *M. langstoni* in the predominantly red brown terga and the basally black pterostigma (Fig. 7A), while the specimens 30767 + 30797 agree with *M. major* in the dorsally predominantly black terga and the unicolorous yellow pterostigma (Fig. 7G).

Several specimens included in the type series of *M. langstoni* were reared from the pecan *Carya illinoinensis* (Ross 1936). Ross (1936) also referred to the descriptions of larvae of *M. major* by Dyar

(1898b) and Yuasa (1923). Dyar described the larvae as "gregarious on the young leaves of hickory" [= *Carya* spec.]. Yuasa (1923) noted "on hickory and pecan". If the association of larvae described by Yuasa as "*Megaxyela* sp. 1" with *M. major* by J.M. Langston and H.H. Ross is correct, *M. major* is a "solitary feeder on pecan and some other hickories" (Ross 1936). Citing *M. major*, *M. langstoni* has been listed as a pest of pecan in Texas, but "in most cases sawfly damage is just 'visual discomfort'

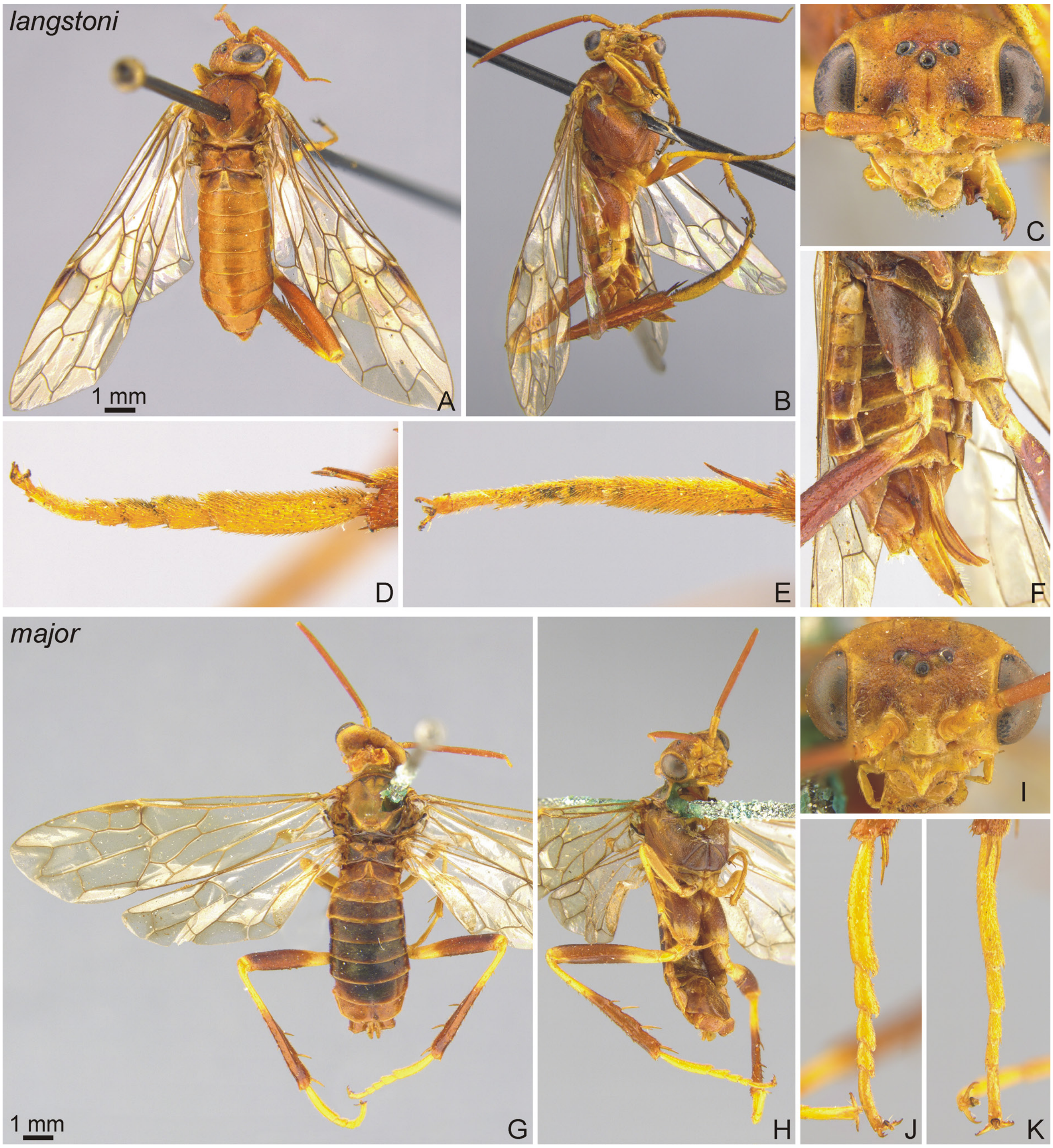

Fig. 7. A–F. *Megaxyela langstoni* Ross, 1936, ♀ (A–C = holotype, DEI-GISHym 30821, INHS; D–F = 30822, USNM). **G–K**. *M. major* (Cresson, 1880), ♂, paratype (30823, ANSP). **A–B**. ♀, holotype, habitus dorsal/lateroventral. **C**. ♀, holotype, head frontal. **D–E**. ♀, metatarsus, lateral/ventral. **F**. ♀, abdomen lateroventral. **G–H**. Habitus dorsal/lateroventral. **I**. Head frontal. **J–K**. Metatarsus lateral/ventral.

where the larvae have damaged some of the new foliage" (Ree 2012, 2014). Significant defoliations, which might justify a treatment, obviously are rare (Ree 2016).

Smith & Schiff (1998) recorded *Megaxyela major* from 14 states of the eastern US. Collection data from Mississippi completely refer to *M. langstoni* (type material and additional specimens). We identified additional material from Oklahoma and Texas. For the distribution of *M. major*, we confirm Kansas (holotype of *Odontophyes ferruginea*), Texas (lectotype of *Xyela major*) and, upon additional specimens studied, also Oklahoma and Pennsylvania. Adults from Florida, Iowa, Missouri, New York and South Carolina need to be re-identified. The state records for Alabama, Arkansas, Georgia, Tennessee and Virginia are based on larvae solely. Since the larvae of four of seven Nearctic *Megaxyela* are unknown, and *Megaxyela* larvae generally display only vague specific differences according to our experience with East Asian taxa, these records require scrutiny. Ross (1936) discriminated the larvae of *M. langstoni* and *M. major* by the presence of a single large dark area vs pairs of black spots on the pronotum and the penultimate abdominal segment. But these character states might also apply to those Nearctic species of *Megaxyela* for which the larvae are still unknown.

Megaxyela major (Cresson, 1880)
Fig. 7G–K

Xyela major Cresson, 1880: 34 (♀, type locality: USA, Texas).
Odontophyes ferruginea Bridwell, 1906: 94 (♀, type locality: USA, Kansas, Baldwin).

Megaxyela major – Ashmead in Dyar 1898a: 214 (combination). — Smith & Schiff 1998: 638–639 (key), 644–648 (description, distribution, hosts, references; including data of *M. langstoni*), figs 4, 7, 18–19, 33.
Odontophyes ferruginea – Ross 1932: 162 (synonymy with *M. major*).

Type material

USA: ♀, lectotype of *Xyela major* (designated by Cresson 1916): "Texas, (Belfrage)" (Cresson 1880) (ANSP, Type No. 330), studied by Smith & Schiff (1998: 646). Cresson (1880) described the abdomen as "blackish-brown above". He did not refer to the pterostigma but noted "nervures ferruginous". Paralectotype ♂ (here studied): "Tex."; "12."; [blue:] "Para-Type 530.2"; "*Megaxyela major* (Cresson) Det. D. Burdick '54"; "DEI-GISHYM 30823"; ANSP. Fragments of fore legs glued to label, head glued to specimen, left antennal filament missing (Fig. 7G–H).

USA: ♀, holotype of *Odontophyes ferruginea*: [red:] "Type ♀ *Odontophyes ferruginea* J. C. Bridwell"; [red:] "*Odontophyes ferruginea* Brid., ♀ TYPE"; "Baldwin Kansas"; "Bridwell Apr."; [handwritten:] "on *Salix* shrub willow"; "USNM Ent 00778020" (USNM). Good shape; left antenna missing beyond scape; right hind tarsus missing. The synonymy with *M. major* by Ross (1932) is here confirmed.

Additional material examined

USA: 1 ♀, Oklahoma, Pawnee County, Pawnee, 352736 East Hwy 64, 36.292° N, 96.716° W, Malaise trap, 23 Apr.–3 May 2011, C. Apgar leg., DEI-GISHym 30767 (specimen used for barcoding) (USNM); 1 ♀, same locality, Malaise trap, 9–23 Apr. 2016, C. Apgar leg., DEI-GISHym 30797 (specimen used for barcoding) (USNM); 1 ♀, Pennsylvania, Huntington, 3 Jun. 1934 (USNM).

Supplementary description

Male

Synantennomere 3 3.7 mm, filament 0.7 mm, with 7 articles. Pulvilli present on metatarsomeres 1–4, on article 1 pulvillus 80 µm long, on article 4 120 µm (Fig. 7J–K). See key for additional characters.

Host plant

Supposedly pecan (*Carya illinoinensis*) and possibly additional *Carya* species (Ross 1936).

Remarks

See *Megaxyela langstoni*.

Megaxyela parki Shinohara, 1992
Figs 1D, 8A–H, 11F, 12F, 13D

Megaxyela parki Shinohara, 1992: 792–794, figs 4C, 4E, 6A–B (♀, type locality: South Korea, Kangwon-do, Mt. Samagsan near Chuncheon).

Material examined or reported in literature

SOUTH KOREA: 1 ♂, Chollanam-do, Sonamsa, 34.98° N, 127.33° E, 19 Apr. 1990, H.-J. Choe leg., DEI-GISHym 710 (CALS); 1 ♀ (holotype, CIS), 4 ♀♀ (paratypes, NSMT), Kangwon-do, Chuncheon,

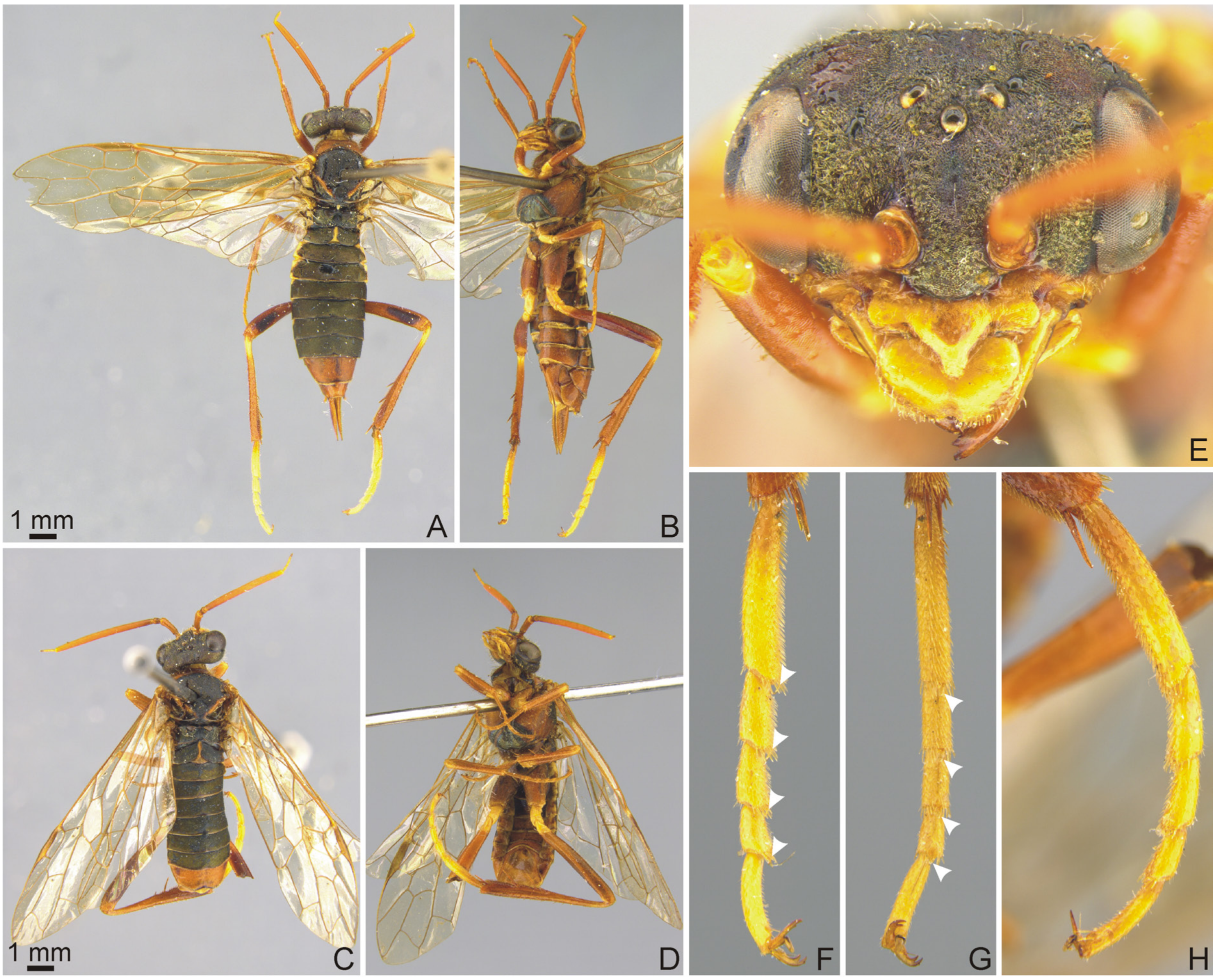

Fig. 8. *Megaxyela parki* Shinohara, 1992. **A–B**. Habitus dorsal/lateroventral (♀, DEI-GISHym 18509, NSMT). **C–D**. Habitus dorsal/lateroventral (♂, 710, NSMT). **E**. Head frontal (♂, 710, NSMT). **F–G**. Metatarsus lateral/ventral, arrowheads indicate pulvilli (♀, 18509, NSMT). **H**. Metatarsus lateral (♂, 710, NSMT).

7.5 km SW, Mt. Samagsan, 37.80° N, 127.68° E, 650 m alt., 9 May 1990, A. Shinohara leg. (Shinohara 1992); 1 ♀, Kangwon-do, Mirugam (Pugdaesa), Mt. Odaesan, 37.80° N, 128.57° E, 1300 m alt., 24 May 1989, A. Shinohara leg. (paratype, USNM) (Shinohara 1992); 1 ♀, same locality, 27 May 1989, A. Shinohara leg., (paratype, NSMT) (Shinohara 1992); 3 ♀♀, same locality, 29 May 1993, A. Shinohara leg., DEI-GISHym 18510 (NSMT); 1 ♀, same locality, 30 May 1993, A. Shinohara leg. (NSMT); 1 ♀, same locality, 31 May 1993, A. Shinohara leg., DEI-GISHym 18509 (NSMT); 1 ♀, same locality, 1 Jun. 1993, A. Shinohara leg. (NSMT).

Description

See Shinohara (1992) and Figs 8A–B, 11F.

Female

Ovipositor about 2.6 mm long, weakly curved ventrally, valvula 1 and valvula 2 without bulbous zone, without ctenidia (Fig. 12F). Pulvilli present on metatarsomeres 1–4, on article 1 pulvillus 130–150 µm long, on article 4 150–180 µm (Fig. 8G–H).

Male

Color. Similar to female (Figs 1D, 8D–E, H). Tergum 8, sterna 4–6, subgenital plate and genitalia red brown, sterna 1–3 black with red brown mark medially.

Morphology. Body 9.8 mm, fore wing 11.5 mm long. POL : OOL : OCL = 1.0 : 1.8 : 1.8. Interantennal distance 1.2 × as wide as distance between torulus and eye margin, malar space 0.4 × as wide as interantennal distance. Eye 1.4 × as long as wide, frons 1.5 × as wide as maximum diameter of eye. Synantennomere 3 4.0 mm, antennal filament 0.8 mm, with 7 articles. Article 3 of maxillary palp 0.5 mm. On hind leg, femur 3.8 mm, tibia 5.1 mm, tarsus 4.3 mm, tarsomere 1 4.5 × as long as wide, longer distal spur of tibia 0.5 × as long as tarsomere 1. Claws and microsculpture similar to female. Subgenital plate bluntly pointed at apex. Valviceps of penis valve distally evenly rounded, basal third of upper side expanded to a round lobe coiled laterally, medial 0.4–0.7 of upper edge with irregular teeth. Distal 0.4 of valviceps with long setae, lower portion of medial 0.4–0.7 with short setae (Fig. 13D).

Remarks

Megaxyela parki belongs to the group of East Asian species with extensively white terga 2–4. Among these species, it is unique in the completely red brown tergum 7 (black and laterally/ventrally white in other species). It is also easily identified by its comparatively short antennae with the antennal filament comprising 6–7 articles, long valvula 3 of the ovipositor sheath, almost completely black head, red brown antennae, and yellow white metatarsus.

The previously unknown male is similar to the female in color. Both male and female bear a much less dense hair cover on the posterior tarsi than other East Asian taxa. The larval host is still unknown.

Megaxyela pulchra Blank, Shinohara & Sundukov sp. nov.

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Figs 9A–I, 11G, 12G, 13E, I

Megaxyela gigantea – Zhelochovtsev & Zinovjev 1995: 396 (misidentification, *partim*). — Lelej & Taeger 2007: 933 (misidentification, *partim*). — Lelej 2012: 62 (misidentification, *partim*).
Megaxyela aff. *gigantea* – Sundukov 2009: 213 (record from Russia, Primorskiy Kray).
Megaxyela sp. 1 – Shinohara *et al.* 2017: fig. 15 (phylogenetic analysis). — Blank *et al.* 2017: 115

Diagnosis

Megaxyela pulchra sp. nov. is characterized by the following unique combination of characters: frons above the antennal toruli rugulose, head with black spot extending from postocellar area and vertex to the antennal toruli, pterostigma yellow brown and infuscate basally and anteriorly, pectus red brown, hypopygium of male red brown.

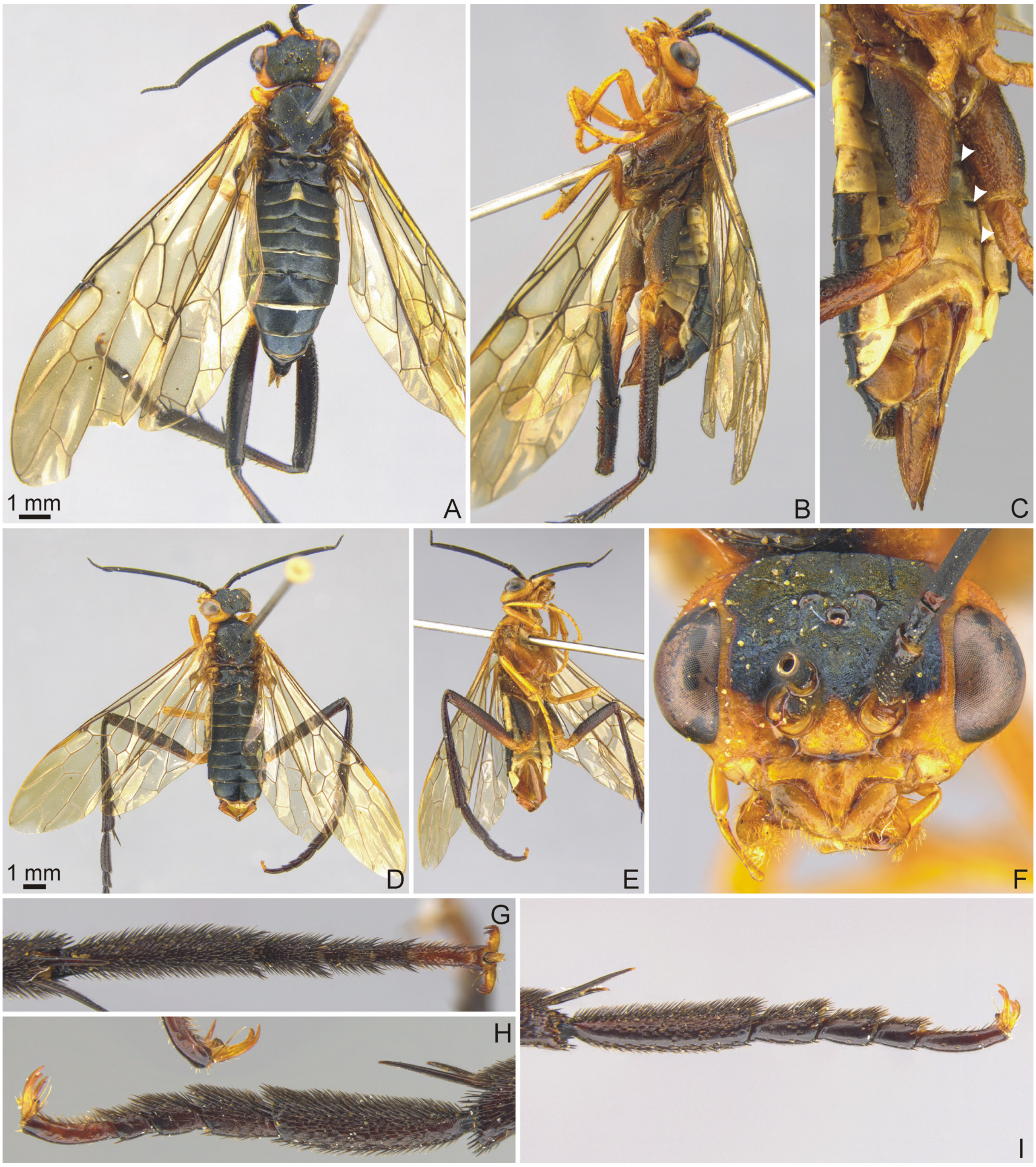

Fig. 9. *Megaxyela pulchra* Blank, Shinohara & Sundukov sp. nov. **A–B**. Habitus dorsal/lateroventral (♀, holotype, DEI-GISHym 86249, ZIN). **C.** Abdomen lateroventral, arrowheads indicating black anterolateral spots on sterna (♀, 18504, NSMT). **D–E**. Habitus dorsal/lateroventral (♂, 22349, NSMT). **F**. Head frontal (♀, holotype, 86249, ZIN). **G–I**. Metatarsus ventral (♀, 22346, NSMT), lateral (♀, 22346, NSMT), lateral (♂, 22349, NSMT).

Etymology

The Latin adjective *pulcher* (fem. *pulchra*) indicates the beauty of this species.

Type material

Holotype

RUSSIA: ♀: "[vertically:] RU012 [horizontally:] RU [= Russia]: Primorskij Kraj: Ussuri Nature Reserve 43.644°N 132.346°E 150 m [alt.] 23. May 2016 leg. Kramp, Prous & Taeger"; [red:] "Holotype *Megaxyela pulchra* sp.n. det. SM Blank 2016"; "DEI-GISHym 86249 (see ethanol coll.)", specimen used for barcoding (pinned specimen in ZIN, right midleg in ethanol collection of SDEI).

Paratypes (11 ♀♀, 4 ♂♂)

CHINA: 1 ♂, Hubei Sheng, Guanmenshan, Shennongjia, 31.43° N, 110.36° E, 21 May 2010, A. Shinohara leg. (NSMT) (specimen DEI-GISHym 18504 used for barcoding); 1 ♂, Jilin Sheng, 43.00° N, 126.00° E, Jul. 1987 (CSCS); 1 ♀, Liaoning Sheng, 41.00° N, 123.00° E, 8 May 1958 (CSCS); 1 ♀, Shaanxi Sheng, Foping County, Daguping, 33.58° N, 107.77° E, 1320 m alt., 28. Apr. 2006, Mojun He leg. DEI-GISHym 22563 (CSCS); 1 ♀, Tibet Autonomous Region, Metok ["Motuo", Mêdok], 29.32° N, 95.32° E, 1050 m alt., 9 Apr. 1980, Yingtao Jin leg. (CSCS).

RUSSIA: 1 ♀, Primorskiy Kray, Anisimovka, 43.17° N, 132.80° E, 26 May 1974, Berezantsev leg. (IBSS); 1 ♀, Primorskiy Kray, Lazovskiy Rayon, Lazo, 43.20° E, 134.15° N, 21–24 May 2008, V. Shokhrin leg. (IBSS); 1 ♀, Primorskiy Kray, Ussuri Nature Reserve, 43.67° N, 132.30° E, 23 May 1994, A. Lelej leg., DEI-GISHym 18501 (NSMT); 1 ♀, Primorskiy Kray, Voroshilovskiy Rayon, Suputinka River, 43.63° N, 132.10° E, 11 Jun. 1935, T. Samoylov leg. (ZIN).

SOUTH KOREA: 3 ♀♀, 2 ♂♂, Kangwon-do, Mirugam (Pugdaesa), Mt. Odaesan, 37.80° N, 128.57° E, 1300 m alt., collected from *Juglans* ?*mandshurica*, 1 Jun. 2002, A. Shinohara leg. (NSMT) (including 1 ♀, 2 ♂♂ DEI-GISHym 18503, 22347, 22349 used for barcoding, also including DEI-GISHym 22346, 22348 illustrated in figures); 1 ♀, same locality, 31 May 1998, A. Shinohara leg. (NSMT).

Description

Female

Color. Body red brown with black and white pattern, black parts with bronze to blue tinge (Fig. 9A–C). Head brown, black spot of frons and vertex ventrally extending to toruli and leaving narrow stripe along inner orbits brown (Fig. 9F). Antenna black, narrow base of scape brown. Thorax with following parts black: Large medial spot on pronotum, complete dorsal side of mesothorax and metathorax, variable marks on dorsal corner of mesepisternum, metepimeron and metepisternum; mesopostnotum posteriorly and lateral mesonotal lobes with shared small brown spot laterally extending to mesoscutellum. Abdomen in dorsal view with continuous white bands laterally on terga 2–3 (each about 0.1 × as wide as tergal width), tergum 4 and 8 with narrower band or inconspicuously white, ventral portions of terga 2–4 and 8 completely white, of terga 5–7 black in dorsal half and white in ventral half, of tergum 9+10 brown (Fig. 9B–C). Sterna white, in two specimens on anterior margin of sterna 1–5 with pairs of black marks each about as wide as ocellar diameter (Fig. 9C), valvifer 2 and valvula 3 brown (tip of valvula 3 black only in holotype, Fig. 11G), membrane between valvifer 2 and valvula 3 pale. Legs brown with following black pattern: stripe on posterolateral margin of mesocoxa, dorsal, lateral and lateral third of ventral side of metacoxa, metafemur except for narrow base and fading stripe from base to middle along ventral side, metatibia and metatarsus. Wing hyaline and weakly brown stained, venation brown, pterostigma yellow brown with narrow base and anterior margin infuscate (Fig. 9A–B).

Morphology. Body 10.8–13.4 mm, fore wing 14.9–16.0 mm long. POL : OOL : OCL = 1.0 : 1.9–2.1 : 1.9–2.0. Interantennal distance 1.0–1.1 × as wide as distance between torulus and eye, malar space

0.6–0.7 × as wide as interantennal distance. Eye 1.3–1.4 × as long as wide, frons at dorsal edge of antennal toruli 1.7–1.8 × as wide as maximum diameter of eye. Synantennomere 3 3.8–4.9 mm, filament 1.2–1.3 mm, with (8–)9–10 articles. Article 3 of maxillary palp 0.4–0.5 mm long. Ovipositor sheath 3.1–3.4 mm, valvula 3 1.5–1.6 × as long as valvifer 2, valvula 3 2.0–2.2 × as long as wide (Fig. 11G). On hind leg, femur 4.6–5.4, tibia 5.3–6.2 mm, tarsus 3.7–4.4 mm, tarsomere 1 4.0–4.3 × as long as wide, longer distal spur of tibia 0.6–0.7 times as long as tarsomere 1, subapical tooth of claw stout and slightly shorter than apical tooth (Fig. 9G–H). Head dull, medial part of frons and vertex minutely areolate, frons above toruli rugulose, gena coriarious. Inner and outer orbits with continuous carina, on inner orbit separating red brown stripe along eye from black spot of frons (Fig. 9F). Mesoscutum and mesoscutellum homogeneously, minutely areolate. Mesepisternum coriarious, shining, with shallow pits. Metatarsomere 1 sparsely setose dorsally and dorsolaterally, densely setose lateroventrally and ventrally, setae up to 200 µm long ventrally. Pulvilli absent on article 1 of metatarsus, present on articles 2–4, on article 4 pulvillus 70 µm long (Fig. 9G–H). Basal and medial sections of valvula 3 of ovipositor sheath convex dorsally, almost straight ventrally, preapical section concave on dorsal and ventral edge, medial to preapical section of dorsal margin and ventral margin with up to 150 µm long setae (Fig. 11G). Ovipositor about 2.8 mm long, weakly curved ventrally, valvula 1 and valvula 2 with bulbous areas close to middle, without ctenidia (Fig. 12G). Valvula 1 in distal 0.6 with very narrowly spaced, subparallel, straight, vertical annuli, ventral edge in distal 0.3 bearing very small serrulae. Valvula 2 in distal 0.6 with narrowly spaced annuli, distal 0.4 of dorsal edge of valvula 1 with small denticles.

Male

Color. Similar to female (Fig. 9D–E). Subgenital plate and genitalia red brown (Fig. 13I).

Morphology. Body 10.2–10.9 mm, fore wing 12.7–13.4 mm long. POL : OOL : OCL = 1.0 : 1.9–2.2 : 1.8–2.0. Interantennal distance 1.0–1.1 × as wide as distance between torulus and eye margin, malar space 0.5–0.6 × as wide as interantennal distance. Eye 1.3–1.4 × as long as wide, frons at dorsal edge of antennal toruli 1.7–1.8 × as wide as maximum diameter of eye. Synantennomere 3 4.4–4.8 mm, filament (1.0–)1.2–1.4 mm, with 9–11 articles (one male with left filament 1.2 mm long, 9 articles, right filament 1.0 mm long, 7 articles). Article 3 of maxillary palp 0.4–0.5 mm. On hind leg, femur 4.3–4.6 mm, tibia 5.2–5.5 mm, tarsus 4.4–4.6 mm, tarsomere 1 4.2–4.8 × as long as wide, longer distal spur of tibia 0.5 × as long as tarsomere 1. Claws, pulvilli and microsculpture similar to female (Fig. 9I). Subgenital plate bluntly pointed at apex. Valviceps of penis valve distally evenly rounded, basal 0.4 of upper side expanded to a round lobe coiled laterally (Fig. 13E), medial 0.4–0.8 of upper margin almost straight, with numerous small teeth. Distal 0.8 of valviceps with long setae, most dense on lower portion in medial 0.2–0.5 (Fig. 13E).

Host plant

In South Korea, A. Shinohara captured two females and three males from *Juglans ?mandshurica*. Host records of *J. ailanthifolia* (cited as *J. sieboldiana*), *J. mandshurica*, *J. regia* (including the synonym *J. sinensis*), *Pterocarya rhoifolia* and *P. stenoptera* stated for *Megaxyela gigantea* by Saito (1941), Ko (1969) and Xiao (2006) might also contain the new species *M. pulchra* sp. nov.

Remarks

Among East Asian *Megaxyela*, this species is morphologically close to *M. togashii*. Both species have the frons above the antennal toruli rugulose (frons microareolate throughout in *M. fulvago* sp. nov. and *M. gigantea*) and extensively black (completely or largely red brown in *M. fulvago* sp. nov. and *M. gigantea*), valvula 3 2.0–2.2 × as long as wide (2.8–3.0 in *M. parki*), pterostigma infuscate basally and anteriorly (unicolorous yellow brown in *M. fulvago* sp. nov., *M. gigantea* and *M. parki*, completely black in *M. euchroma* sp. nov.), basal lobe of valviceps small and distally truncate, upper edge medially almost straight and lacking large teeth, long setae present on the lower portion in the medial 0.2–0.5

(basal lobe more prominent in *M. euchroma* sp. nov., *M. fulvago* sp. nov., *M. gigantea* and *M. parki* sp. nov., upper edge raised medially in *M. gigantea*, large teeth on the upper edge present particularly in *M. euchroma* sp. nov., long setae absent in medial portion of valviceps in *M. euchroma* sp. nov. and *M. parki* sp. nov.).

Megaxyela pulchra sp. nov. differs from the Nearctic species of *Megaxyela*, except for *M. langstoni* and *M. major*, and from the East Asian *M. euchroma* sp. nov. in the presence of a broad, continuous white band dorsolaterally and ventrally on terga 2–3. Such extensive white pattern on the basal terga is absent in most North American species, which at most bear a narrow white stripe along the ventral margin of the terga as observed in *M. alisonae*, *M. bicoloripes* and *M. tricolor* (Smith & Schiff 1998; Blank, unpublished data). *Megaxyela pulchra* sp. nov. differs from *M. langstoni* and *M. major*, for example, in the black metatarsus (yellow white in *M. major*) and in the stout valvula 3 of the ovipositor sheath (Fig. 11G; slender in *M. major*, see Smith & Schiff 1998: fig. 7).

Morphological differences between *M. pulchra* sp. nov. and *M. togashii* are faint: the mesoscutellum is homogeneously areolate and flat in *M. pulchra* sp. nov., but areolate in the middle, with a wide stripe along lateral and anterior margin rugose with areolate microsculpture in *M. togashii*; the distance between the toruli is 0.95–1.05 × as wide as the distance between torulus and eye margin in *M. pulchra* sp. nov. ♀ but 1.20 × in *M. togashii* ♀; the malar space is 0.6–0.7 × as wide as the distance between toruli in *M. pulchra* sp. nov. but 0.4 in *M. togashii*. The two species exhibit different tendencies of coloration: the face, ventral part of mesepisternum and mesosternum, and dorsal portion of tergum 4 are paler in *M. pulchra* sp. nov., while the posteriolateral ridge of the mesoscutal lateral lobe is paler in *M. togashii*. The subgenital plate of the male *M. pulchra* sp. nov. is red brown as in *M. gigantea*, whereas it is white in the male *M. togashii*.

The anterior margins of the sterna always bear a pair of large black marks in *M. togashii*. Such marks are absent in other *Megaxyela* (see Smith & Schiff 1998 for Nearctic species) except for *M. pulchra* sp. nov., whose female rarely bears small marks on the sterna. These spots are a putative apomorphy of the vicariant species *M. pulchra* sp. nov. from the East Asian mainland and *M. togashii* from Japan. Among Xyelidae, similar pairs of sibling species (or at least morphologically very similar species) with East-Asian mainland / Japanese vicariance have been observed among *Xyela* species associated with Japanese red pine, *Pinus densiflora* Siebold & Zuccarini (Blank *et al.* 2005).

The specimens studied genetically are supported by a bootstrap of 100%. The maximum intraspecific variation is 3.1%. The nearest neighbor, *M. togashii*, is placed at a minimum pairwise distance of 8.0%.

Zhelochovtsev & Zinovjev (1995), Lelej & Taeger (2007) and Lelej (2012) listed *M. gigantea* for the Russian Far East, but at least the female from Voroshilovskiy Rayon identified by A. Zinovjev refers to *M. pulchra* sp. nov. Sundukov (2009) noted a specimen from Lazo differing from *M. gigantea*, which is included as a paratype of *M. pulchra* sp. nov. here. The specimens published by Shinohara (1992) for South Korea all belong to *M. gigantea*.

Megaxyela togashii Shinohara, 1992
Figs 10A–J, 11H, 12H, 13F

Megaxyela togashii Shinohara, 1992: 789–792, 794, figs 1C–D, 2C–D, 2F–G, 4B, 4D, 5A–C (♀♂, type locality: Japan, Honshu, Ishikawa Prefecture, Yoshinodani-mura, Senami).

Megaxyela togashii – Tanaka 1999: 57 (record from Japan, Honshu, Yamaguchi Prefecture). — Yamada 2000: 53 (record from Japan, Honshu, Aomori Prefecture). — Naito *et al.* 2004: 6 (record from

Japan, Honshu, Hyogo Prefecture). — Shinohara 2006: 157 (record from Japan, Shikoku, Ehime Prefecture). — Shinohara *et al.* 2017: 222–230 (record from Japan, Hokkaido, larva, life history).

Megaxyela gigantea – Watanabe 1992: 8 (record from Japan, Honshu, Okayama Prefecture). [See Ko (1969), Smith (1978) and Shinohara (1992) for numerous additional references].

Material examined or reported in literature

JAPAN: 6 larvae, Hokkaido, Ashoro town, Asahi, 43.233° N, 143.500° E, 100 m alt., 30 Jun. 2010, A. Shinohara and H. Hara leg., on *Juglans ailanthifolia*, including DEI-GISHym 30805–30807 (NSMT) (Shinohara *et al.* 2017); 2 larvae, Hokkaido, Ashoro town, Nishikitoushi, 43.383° N, 143.367° E, 345 m alt., 1 Jul. 2010, A. Shinohara and H. Hara leg., on *Juglans ailanthifolia* ,including DEI-GISHym 30804 (NSMT) (Shinohara *et al.* 2017); 1 larva, Hokkaido, Shintoku town, 43.083° N, 142.817° E, 200 m alt., 26 Jun. 2011, H. Hara leg. (Shinohara *et al.* 2017); 1 larva, Hokkaido, Sapporo city, Misumai, 42.950° N, 141.250° E, 160 m alt., 19 Jun. 2013, H. Hara leg. (Shinohara *et al.* 2017); 1 larva, Hokkaido, Sapporo city, Koganeyu, 42.967° N, 141.200° E, 250 m alt., 19 Jun. 2013, H. Hara leg. (not preserved) (Shinohara *et al.* 2017); 1 ♀, Honshu, Aomori Prefecture, Minami-Hakkoda, 40.60° N, 140.84° E,

Fig. 10. *Megaxyela togashii* Shinohara, 1992, ♀, holotype, DEI-GISHym 22352 (NSMT); ♂, 22354, (NSMT). **A–B**. Habitus dorsal/lateroventral (♀). **C**. Head frontal (♀). **D–E**. Habitus dorsal/lateroventral (♂). **F**. Head frontal (♂). **G–H**. Metatarsus lateral/ventral (♀). **I–J.** Metatarsus lateral/ventral (♂). Arrows in Fig. 10B and 10F indicate dark spots of abdominal sterna, arrowheads in H and J indicate minute pulvilli.

30 May 1999, M. Yamada leg., M. Yamada coll. (Yamada 2000; reliable record, not re-examined); 1 ♂, paratype, Honshu, Hiroshima Prefecture, Kamiyama, Kure, 34.28° N, 132.57° E, 7 May 1933, coll. Nakanishi (UOP) (Shinohara 1992); 1 ♀, Honshu, Hyogo Prefecture, Sayo-gun, Mikazuki-cho, Mihara, 34.95° N, 134.42° E, 18 May 1995, T. Sasai leg., DEI-GISHym 22353 (KUEL) (Naito 2004); 1 ♀, Honshu, Hyogo Prefecture, Shiso-gun, Haga-cho, Akasai-keikoku, 35.23° N, 134.48° E, 680 m alt., 8 Jun. 1986, T. Morita leg., T. Morita coll. (Naito *et al.* 2004; reliable record, not re-examined); 1 ♀, holotype, Honshu, Ishikawa Prefecture, Yoshinodani-mura, Senami, 36.32° N, 136.65° E, 29 Jun. 1964, I. Togashi leg., DEI-GISHym 22352 (NSMT) (distal articles of right antenna glued to collecting label; Shinohara 1992); 5 larvae, 1 egg, Honshu, Hyogo prefecture, Tatsuno city, Shingu town, 34.867° N, 134.567° E, 35 m alt., 30 Apr. 2016, on *Juglans ailanthifolia*, A. Shinohara leg., including Shinohara's sample numbers 761–764 (NSMT) (Shinohara *et al.* 2017); 1 ♀, Honshu, Okayama Prefecture, Kawakami-gun, Bichu-cho, Nishiyuno, 34.80° N, 133.47° E, 5 May 1986, A. Watanabe leg., A. Watanabe coll. (Watanabe 1992, misidentified as *M. gigantea*); 1 ♂, Honshu, Okayama Prefecture, Tamagashi, Okayama-shi, 34.72° N, 133.97° E, 10 m alt., 3 May 2005, A. Shinohara leg., DEI-GISHym 22354, used for barcoding (NSMT) (Shinohara 2006); 1 ♂, as preceding, except 2 May 2006, DEI-GISHym 22521 used for barcoding (NSMT) (Shinohara 2006); 1 specimen, Honshu, Yamaguchi Prefecture, Kuga-gun, Nishiki-machi, Mt. Jakuchi-san, Sancho [= summit], 34.47° N, 132.05° E, 1337 m alt., 6 Jun. 1993, K. Tanaka leg., K. Tanaka coll. (Tanaka 1999, reliable record, not re-examined); 2 larvae, Shikoku, Ehime prefecture, Kihoku town, Narukawa-keikoku, 33.200° N, 132.617° E, 650 m alt., 5 May 2016, on *Juglans ailanthifolia*, A. Shinohara leg., Shinohara's sample numbers 765–766 (NSMT) (Shinohara *et al.* 2017); 1 ♀, Shikoku, Ehime Prefecture, Narukawa-keikoku, Kihoku-cho, 33.20° N, 132.62° E, 550 m alt., 8 May 2006, A. Shinohara leg. (NSMT) (Shinohara 2006).

Description

See Shinohara (1992) and Figs 10A–C, G–H, 11H (ovipositor sheath).

Female

Ovipositor about 2.4 mm long, weakly curved ventrally, valvula 1 and 2 with bulbous areas close to middle, without ctenidia (Fig. 12H). Body 12.6 mm, fore wing 15.4 mm long. Black spot on face extending lateroventrally to mid-level of toruli, medially continuous with predominantly black subantennal area (holotype with two small brown spots) or subantennal area yellow (specimen from Mihara). Pulvilli absent on article 1 of metatarsus, present on articles 3–4, presence ambiguous for article 2, on article 4 pulvillus 70 µm long.

Male (specimen from Tamagashi, DEI-GISHym 22354, Fig. 10D–F, I–J)

Body 12.0 mm, fore wing 13.4 mm. Antennal filament 1.3 mm long, with 8–9 articles. Valviceps distally parabolically rounded, basal quarter of upper side expanded to a round lobe weakly coiled laterally, section of upper edge distal of lobe straight or with shallow elevations, close to the lobe with irregular teeth, in medial 0.3–0.8 with numerous small teeth. Distal 0.7 of valviceps with long setae, dense in medial and lower portion of middle (Fig. 13F).

Host plant

Ten larvae identified by their COI sequences as *M. togashii* were found feeding on *Juglans ailanthifolia* (Shinohara *et al.* 2017). In addition, three adults were collected from trees of this walnut species (Shinohara 2006, citing the synonym *J. mandshurica* Maxim. ssp. *sieboldiana* [Maxim.] Kitamura). Japanese Wingnut, *Pterocarya rhoifolia* Sieb. & Zucc., possibly represents an additional larval host (Shinohara *et al.* 2017). Takeuchi's (1949) record of *Juglans* for *M.* '*gigantea*' (= *M. togashii*) in a checklist of the host plants of Japanese sawflies most likely concerns Saito's (1941) rearing record for *M. gigantea* from Korea (see also Takeuchi 1938).

Remarks

Megaxyela togashii is the correct name for the Japanese species, which has been called *M. gigantea* by Takeuchi (1937), Togashi (1965) and subsequent authors up to Shinohara (1992). This species is most similar to *M. pulchra* sp. nov. in structure and color. See Remarks there for differentiation of these two species.

The clade including two genetically studied adults from Honshu, which were collected on the same site, is supported by a bootstrap of 100%. The maximum intraspecific variation is 1.4%. Under a wider geographical scope, Shinohara *et al.* (2017) observed a variation of 4.3% after inclusion of ten larvae from Hokkaido, Honshu and Shikoku. Even then the intraspecific variation is smaller than the minimum pairwise distance of 8.0% to the nearest neighbor, *M. pulchra* sp. nov.

Megaxyela tricolor (Norton, 1862)

Xyela tricolor Norton, 1862: 144 (♂, type locality: USA, Kansas).

Megaxyela tricolor – Ross 1932: 162–163 (combination, description, key, distribution). — Smith & Schiff 1998: 638–639 (key), 648 (description, distribution, references), figs 11, 22–25, 35.

Material examined

USA: 1 ♀, West Virginia, Upshur County, Ruraldale, 12 Apr. 2014, photographed by S. Cresswell (Cresswell 2014).

Supplementary description

See Smith & Schiff (1998). Female. Antenna black. Metafemur orange with extreme apex on outer surface black (1 ♀ studied by Smith & Schiff 1998) or distal 0.4 black (Cresswell 2014).

Remarks

This is the first state record for West Virginia. The species has been found in Connecticut, Illinois, Kansas, Missouri and in Ontario (Smith & Schiff 1998).

Identification key to the species of *Megaxyela*

1 a Valvula 3 of ovipositor sheath dorsally straight, ventrally evenly convex in basal and medial portion Fig. 11D).
b Ovipositor curved dorsally (Fig. 12D).
Male unknown. USA (West Virginia) ……………… ***M. inversa*** Blank & D.R. Smith sp. nov.
– aa Valvula 3 of ovipositor sheath dorsally convex, ventrally various in shape (Fig. 11A–C, E–H; Smith & Schiff 1998: figs 7–11).
bb Ovipositor curved ventrally (Fig. 12A–B, E–H, Smith & Schiff 1998: figs 16–23, 26–27) ……2

2(1) a East Palaearctic and Oriental species ……………………………………………………3
– aa Nearctic species ……………………………………………………………………8

3(2) a Tergum 8 red brown (Fig. 8A, D).
b Eye surrounded by black except for red brown malar space (Fig. 8F).
c Antenna red brown (Figs 1D, 8A–D).
d Claw of hind leg with large subapical tooth (Fig. 8F–G).
South Korea (Fig. 14) …………………………………………***M. parki*** Shinohara, 1992

– aa Tergum 8 black (e.g., Fig. 3A, D), sometimes laterally and ventrally white (e.g., Figs 4A, 5A–D, 9C).
bb Eye at least narrowly lined with yellow or red brown on inner and outer orbits (Figs 3F, 9F, 10C–D) or face predominantly pale (Figs 4G, 5E).
cc Dorsal side of antenna black.
dd Claws bifid (e.g., Figs 3H–I, 4D, 5G) ……………………………………………………4

4(3) a Metatarsus white, base of metatarsomere 1 black (Fig. 3A–B, D–E, H–I, K).
b Terga 2–6 with narrow, evenly wide line along ventral margin (Fig. 3C), terga 2–4 laterally black in dorsal view (Fig. 3A, D).
c Head black, inner and outer orbits with narrow yellow lines, vertex with linear yellow spot (Fig. 3F–G).
d Pulvillus present on metatarsomere 1 (Fig. 3I–K).
e Mesepisternum with indistinct pits between minutely areolate microstructure, dull.
f Antennal filament composed of 7–8 (rarely 9) articles.
g ♀: Ovipositor sheath black except for brown basal half of valvifer 2 (Fig. 11A).
h ♀: Ovipositor with ctenidia along annuli (Figs 1F, 12A).
i ♂: Hypopygium black (Fig. 3E).
China (Zhejiang) (Fig. 14) ……………………***M. euchroma*** Blank, Shinohara & Wei sp. nov.
– aa Metatarsus black (e.g., Figs 4A–F, 5C–H).
bb Terga 2–3 or 2–4 with broad white band on dorsolateral and complete ventral portion, terga 3–5 or 4–5 less extensively white than preceding terga (Figs 4A, E–F, 5A–D, 9A–E, 10A–B, E–F).
cc Head more extensively red brown or yellow, at least gena and face below antennal toruli pale (Figs 4G, 5E, 9F, 10C–D).
dd Pulvillus absent on metatarsomere 1.
ee Mesepisternum with distinct pits, smooth or with coriarious microstructure, more or less shining.
ff Antennal filament composed of 9–10 articles (rarely fewer articles present on one antenna, check both antennae).
gg ♀: Ovipositor sheath red brown, valvifer 2 sometimes white, valvula 3 sometimes infuscated along dorsal margin (Fig. 11C, G–H).
hh ♀: Ovipositor without ctenidia along annuli (Fig. 12B–C, G–H).
ii ♂: Hypopygium red brown (Figs 4F, 5D, 9E) or white (Fig. 10F) ……………………………5

5(4) a Head, prothorax and mesothorax red brown, without black (Fig. 4A, E–G).
China (Hunan, Jiangsu, Zhejiang) (Fig. 14) …***M. fulvago*** Blank, Shinohara & Wei sp. nov.
– aa At least mesoscutum and usually vertex partly black (e.g., Figs 5A, C, 10A, E) ……6

6(5) a At least ventral half of frons red brown (Fig. 5E).
b Pterostigma unicolorous yellow brown (Fig. 5A, C).
c Upper part of gena weakly imbricate, almost smooth, shining (Fig. 5B).
d Microsculpture of frons above antennal toruli minutely areolate, similar to microsculpture of vertex, with few shallow pits (Fig. 5E).
e Dorsal side of terga 2–4 with evenly wide, white lateral margins (Fig. 5A, C).
North and South Korea, Russia (Primorskiy Kray) (Fig. 14) ……***M. gigantea*** Mocsáry, 1909
– aa Black spot of frons ventrally extending to antennal toruli (Figs 9F, 10C–D).
bb Pterostigma yellow brown, narrow at base and anterior margin infuscate (e.g., Figs 9A, 10A).
cc Upper part of gena strongly imbricate, dull.

dd Microsculpture of frons above antennal toruli rugulose, different from areolate microsculpture of vertex (Figs 9F, 10C–D).
ee White lateral margin on dorsal side of tergum 4 narrower than on terga 2–3 or absent (e.g., Figs 9A–E, 10E) 7

7(6) a Mesonotum black or with a small brown spot lateral to mesoscutellum (Fig. 9A, D).
b Preapical sterna white (Fig. 9B, E), sometimes with pair of small black marks on anterior margin (Fig. 9C).
c ♀: Thorax ventrally red brown (Fig. 9B, E).
d ♀: Ovipositor sheath red brown, sometimes tip of valvula 3 black (Fig. 11G).
e ♂: Hypopygium red brown (Fig. 9E).
China (Jilin, Liaoning, Shaanxi, Tibet), South Korea, Russia (Primorskiy Kray) (Fig. 14) ....***M. pulchra*** Blank, Shinohara & Sundukov sp. nov.
– aa Mesonotum black with yellow stripes along posterolateral ridge on mesoscutal lateral lobe (Fig. 10A, E).
bb Sterna red brown to white, preapical sterna with pair of large black marks on anterior margin (Fig. 10B, F).
cc ♀: Mesepisternum red brown, black spot in dorsal corner, black stripe along pectus, pectus largely black medially (Fig. 10B).
dd ♀: Ovipositor sheath red brown with valvifer 2 ventrally yellow white, and valvula 3 with black stripe along dorsal margin (Fig. 11H).
ee ♂: Hypopygium white (Fig. 10F).
Japan (Hokkaido, Honshu, Shikoku) (Fig. 14) ....***M. togashii*** Shinohara, 1992

8(2) a Metafemur, tegula and abdomen black, sterna with indistinctly pale posterior margins.
b Tarsomeres (2–)3–5 of hind legs white.
Canada (Ontario), USA (Indiana, Kansas, Massachusetts, Mississippi, Missouri, New York, Oklahoma, Pennsylvania) ....***M. aviingrata*** (Dyar, 1898)
– aa Metafemur red brown, sometimes apex narrowly black (e.g., Smith & Schiff 1998, fig. 3). Tegula white. Sterna red brown *and/or* posterior margins of terga and sterna white.
bb Metatarsus sometimes completely black (e.g., Smith & Schiff 1998: figs 14 and 15) 9

9(8) a Head yellow and red brown, pronotum red brown (Fig. 7A–C, G–I).
b Metatibia red brown or black, basal 0.2–0.4 white (Fig. 7A–B, F–H) 10
– aa Head (except for clypeus, labrum, mouthparts, mandible) and pronotum black (e.g., Smith & Schiff 1998: fig. 3).
bb Metatibia entirely black (e.g., Smith & Schiff 1998: fig. 3) 11

10(9) a Basal 0.3–0.5 of pterostigma black, distal portion red brown (Fig. 7A–B).
b Dorsal side of terga red brown, terga 1(–2) medially more or less infuscate (Fig. 7A).
c Basal 0.05–0.10 of metafemur yellow white (Fig. 7B, F).
d Distal preapical metatibial spur reaches apex of metatibia (Fig. 7B), inner apical metatibial spur 0.5 × as long as metatarsomere 1 or longer (Fig. 7D–E).
USA (Mississippi, Oklahoma, Texas) ....***M. langstoni*** Ross, 1936 sp. rev.
– aa Pterostigma uniformly red brown (Fig 7G).
bb Dorsal side of terga 1–7 predominantly black (Fig. 7G).
cc Basal 0.30–0.35 of metafemur yellow white (Fig. 7H).
dd Distal preapical metatibial spur not reaching apex of metatibia (Fig. 7H), inner apical metatibial spur about 0.4 × as long as metatarsomere 1 (Fig. 7J–K).
USA (Kansas, Oklahoma, Pennsylvania, Texas) ....***M. major*** (Cresson, 1880)

11(9) a Terga 1–7(–8) red brown, distal margins narrowly infuscate (Smith & Schiff 1998: fig. 3).
b Metatarsomere 1 stout, 4 × as long as wide, pilosity dorsally *and* ventrally dense (Smith & Schiff 1998: fig. 15).
USA (New York, Ohio) ……………………………***M. alisonae*** D.R. Smith & Schiff, 1998
– aa Terga black, distal margins narrowly white.
bb Metatarsomere 1 slender, 6–7 × as long as wide, pilosity dorsally sparse and ventrally dense (e.g., Smith & Schiff 1998: fig. 14) ……………………………………………………………12

12(11) a Metatarsomeres (2–)3–5 white.
b Ventral side of thorax and sterna red brown.
c Alvula 2 less than 3.0 × as long as wide, 0.6 × as long as metatarsus (Smith & Schiff 1998: fig. 10).
USA (Michigan, Mississippi, Missouri, Pennsylvania, Virginia, West Virginia) ……………… ……………………………………………………………***M. bicoloripes*** (Rohwer, 1924)
– aa Metatarsus black.
bb Ventral side of thorax and sterna black, sterna with white distal margins.
cc Valvula 2 4.5 × as long as wide, about as long as metatarsus (Smith & Schiff 1998: fig. 11).
Canada (Ontario), USA (Connecticut, Illinois, Kansas, Missouri, West Virginia) ………… ……………………………………………………………………***M. tricolor*** (Norton, 1862)

Discussion

Megaxyela is a morphologically well-defined genus of Macroxyelinae that also includes two Nearctic species of *Macroxyela* in the extant fauna. The carina along the inner orbit (e.g., Figs 3F–G, 4G, 6C, 8E) is a unique character of *Megaxyela* among Xyelidae. In addition, the comparatively distal position of vein Sc2 of the fore wing (Figs 1A–B, 6F) and the extended hind legs (e.g., Fig. 3A–B, D–E) support this taxon morphologically. In the female the long hind legs may have provided the evolutionary predisposition for a derived oviposition behavior as observed by Saito (1941) in *Megaxyela gigantea* (Shinohara 1992). The monophyly of *Megaxyela* is also corroborated by the analysis of COI sequences: the nearest neighbors *Megaxyela langstoni* and *Macroxyela ferruginea* are separated by a pairwise distance of 13.7%, which is only slightly larger than some interspecific gaps within *Megaxyela* (Fig. 2).

The branching of the cladogram in Fig. 2, which is based on genetic data from a restricted number of *Megaxyela* species, can partly be interpreted with help of morphological characters. *Megaxyela fulvago* sp. nov., *M. gigantea*, *M. pulchra* sp. nov. and *M. togashii* are included in a common clade, which is supported by the presence of bulbous areas on valvula 1 and valvula 2 of the ovipositor (Fig. 12B–C, E, G–H). Such an area is absent in the Nearctic taxa (Figs 7F, 12D; Smith & Schiff 1998: figs 16–29), in the East Asian *M. euchroma* sp. nov. and *M. parki* (Fig. 12A, F) and in *Macroxyela* (Smith & Schiff 1998: figs 30–32). *Megaxyela pulchra* sp. nov. and *M. togashii* share black spots on the anteriolateral side of the sterna (Figs 9C, 10B, F), that may be absent in *M. pulchra* sp. nov. *Megaxyela fulvago* sp. nov. and *M. gigantea* have in common the dull, minutely areolate and shallowly pitted face (Figs 4G, 5E). *Megaxyela langstoni* is very close to *M. major* in structure and color (Fig. 7). Although Smith & Schiff (1998) already casted some doubt, these two taxa were treated as synonyms until now. Even more surprising in the course of this study was the discovery of a very large genetic distance (13.5%) between these species, which led to the recognition of *M. langstoni* as a separate species. Equally large interspecific genetic gaps have been reported for *Pleroneura* and *Xyela* by Blank *et al.* (2013) and Schmidt *et al.* (2017).

Since *Megaxyela* has been collected rarely, only seven of thirteen known species could be analyzed genetically. Among these, the barcoding sequence of *M. gigantea* is very short and supposedly causes the (mis)placement of this species inside the clade of *M. fulvago* sp. nov. An exhaustive scoring of

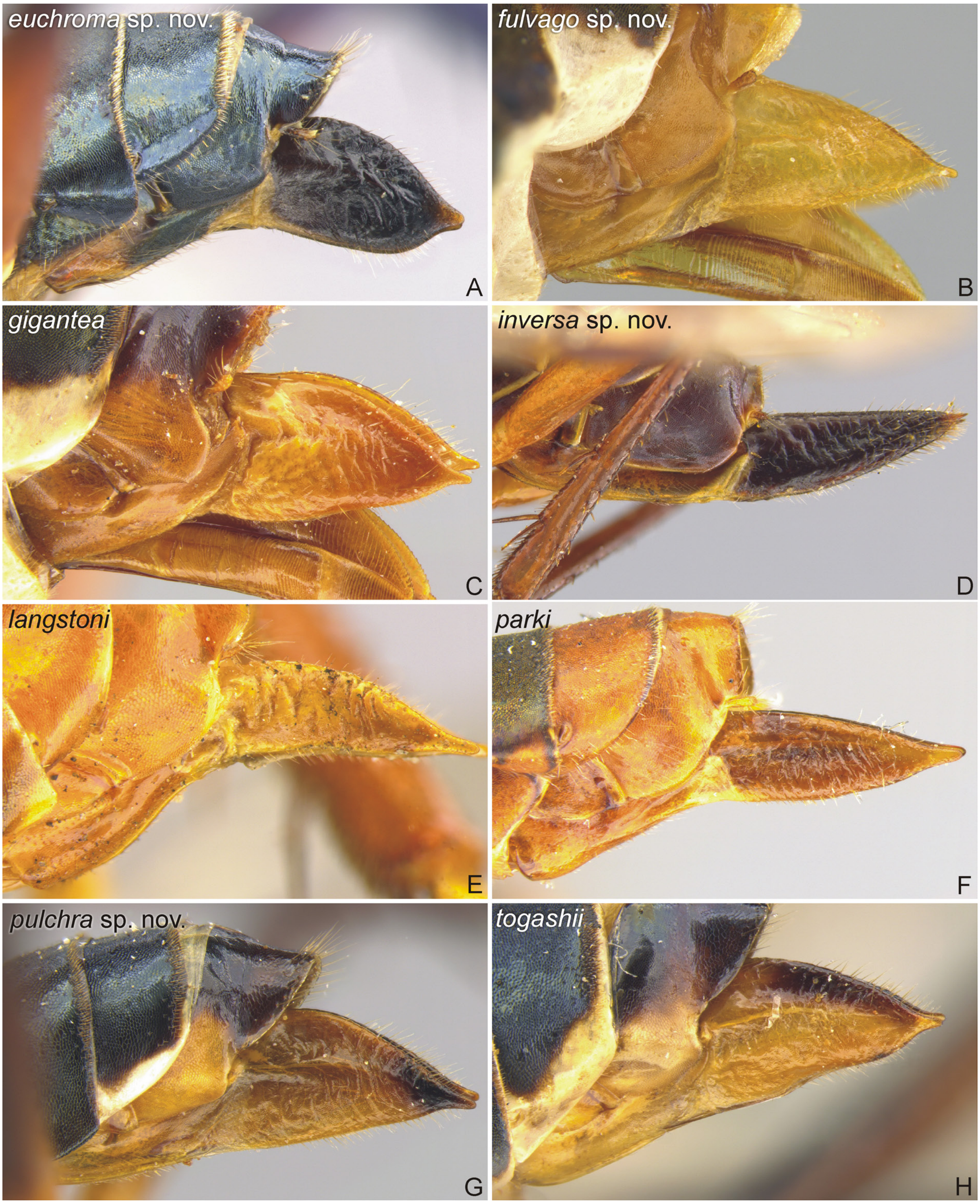

Fig. 11. Species of *Megaxyela* Ashmead, 1898, ovipositor sheaths. **A**. *M. euchroma* Blank, Shinohara & Wei sp. nov. (holotype, DEI-GISHym 22554, CSCS). **B**. *M. fulvago* Blank, Shinohara & Wei sp. nov. (5752, NSMT). **C**. *M. gigantea* Mocsáry, 1909, holotype of *M. mikado* Sato, 1930 (22350, NSMT). **D**. *M. inversa* Blank & D.R. Smith sp. nov., paratype (22356, USNM). **E**. *M. langstoni* Ross, 1936, holotype (30821, INHS). **F**. *M. parki* Shinohara, 1992 (18510, NSMT). **G**. *M. pulchra* Blank, Shinohara & Sundukov sp. nov., holotype (18501, NSMT). **H**. *M. togashii* Shinohara, 1992, holotype (22352, NSMT). Images not to the same scale.

Fig. 12. Species of *Megaxyela* Ashmead, 1898, ovipositors. **A**. *M. euchroma* Blank, Shinohara & Wei sp. nov., paratype, DEI-GISHym 22510 (NSMT). **B–C**. *M. fulvago* Blank, Shinohara & Wei sp. nov., paratype (5752, NSMT). C. Complete valvula 2 (incident light) and tip of valvula 2 (insert, transmitted light). **D**. *M. inversa* Blank & D.R. Smith sp. nov., paratype (22356, USNM). **E**. *M. gigantea* Mocsáry, 1909, holotype of *M. mikado* Sato, 1930 (22350, NSMT). **F**. *M. parki* Shinohara, 1992, paratype (18510, NSMT). **G**. *M. pulchra* Blank, Shinohara & Sundukov sp. nov., paratype (22348, NSMT). **H**. *M. togashii* Shinohara, 1992 (22353, NSMT). The images in B and H have been flipped horizontally.

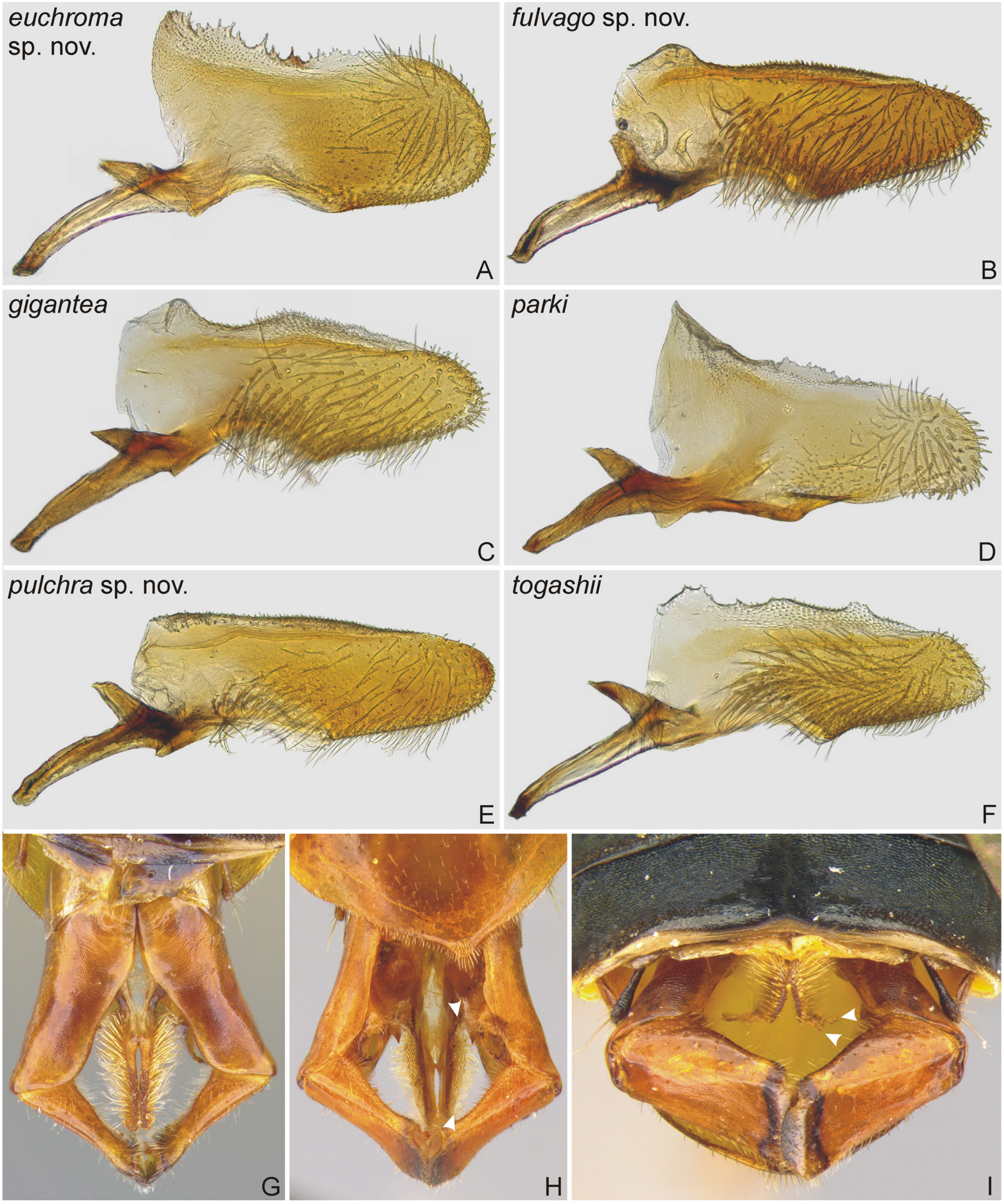

Fig. 13. Species of *Megaxyela* Ashmead, 1898, penis valves (A–F) and genitalia capsules (G–I). **A**. *M. euchroma* Blank, Shinohara & Wei sp. nov. (DEI-GISHym 22513, NSMT). **B**. *M. fulvago* Blank, Shinohara & Wei sp. nov. (5239, NSMT). **C**. *M. gigantea* Mocsáry, 1909 (708, NSMT). **D**. *M. parki* Shinohara, 1992 (710, NSMT). **E**. *M. pulchra* Blank, Shinohara & Sundukov sp. nov. (18503, NSMT). **F**. *M. togashii* Shinohara, 1992 (22521, NSMT). **G–H**. *M. gigantea*, genitalia capsule in dorsal/ventral view (18507, NSMT). **I**. *M. pulchra* sp. nov., genitalia capsule in dorso-posterior view (22349, NSMT). Arrow heads in Fig. 13H–I indicate lobe of upper side of valviceps coiled laterally. Images not to same scale.

morphological characters and the phylogenetic analysis of these data is required to gain a cladogram covering all *Megaxyela* species. This hypothesis might help to explain the evolution of characters like the number of tarsal pulvilli, the shape of the claw, the pilosity of the metatarsus and the color pattern of the abdomen, which show striking differences among the species. Additional barcoding sequences may be particularly significant for the identification of the larvae of *Megaxyela*, which remain poorly known. Proper knowledge of the larvae may provide supplementary data about distribution and host associations of the species.

Successful collecting of *Megaxyela* very much depends on luck, and several species appear to be very rare. The only two known specimens of *M. inversa* sp. nov. were collected at a time interval of 121 years. For most cases, single specimens were collected from undergrowth or lower branches of various plants, resembling the collection circumstances in many other sawflies. A number of unidentified larvae have been found on lower branches at a hight of 1–5 meters. Once, more than 50 adults of *M. gigantea* were collected at Mt. Nogodan, Korea, in 1996 within about 30 minutes. Those adults were flying around a single, unidentified tree near a road, but no specimens were observed on other trees nearby. A subsequent visit at this site in 1997, during exactly the same season, was unsuccessful (Shinohara, personal observations).

The record of *M. fulvago* sp. nov. from Hunan represents the most southern of a *Megaxyela* species in East Asia, extending the known distribution of *Megaxyela* in East Asia 600 km farther south (Fig. 14). The records of *M. pulchra* sp. nov. from Daguping (Shaanxi) and Metok (Tibet) and the record of an

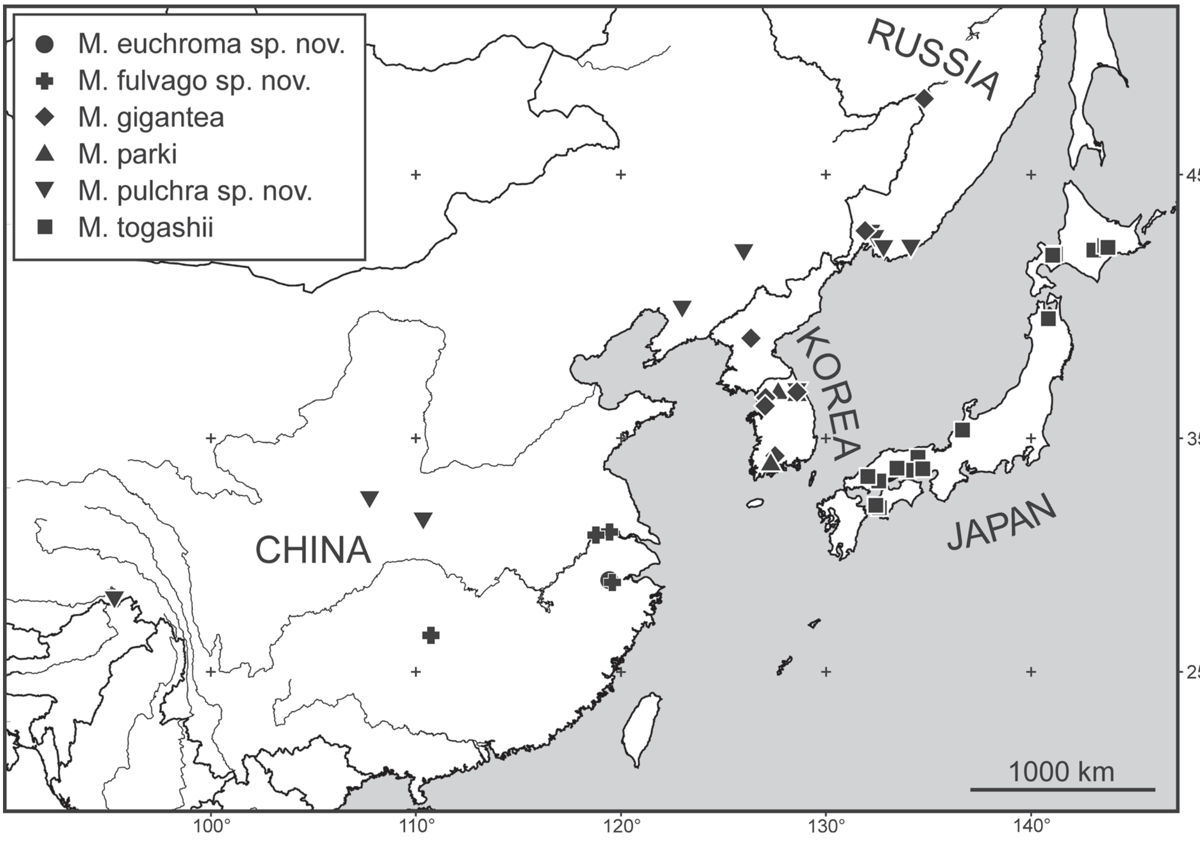

Fig. 14. Distribution of species of *Megaxyela* Ashmead, 1898 in East Asia. Records of *M. togashii* Shinohara, 1992 include reliable records published by Shinohara (1992, 2006), Tanaka (1999), Yamada (2000), Naito *et al*. (2004) and Shinohara *et al.* (2017). Other distribution data are based on examination of material in course of this work.

unidentified *Megaxyela* larva from Gongshan (Yunnan; specimen illustrated by Taeger *et al.* 2010: pl. 21 fig. 3) extend the known distribution area of East Asian *Megaxyela* more than 2500 km westwards with regard to previously published data. Juglandaceae also occur in northern Burma and India (Lu *et al.* 1999) as well as in more western regions of Eurasia, but *Megaxyela* has never been recorded from there. In the Nearctic realm, extant *Megaxyela* and chiefly also their hosts occur in the East, leaving a striking gap in the West of the Nearctic or in the West of the Palaearctic in view of the global distribution. The record of †*M. petrefacta* and †*Carya florissantensis* Manchester from Oligocene deposits of Florissant (Colorado) and additional records of fossil Juglandaceae from the western USA (Brues 1908; Manchester 1987) indicate that in the extant fauna both these sawflies together with their hosts exhibit a relict distribution. A thorough phylogenetic analysis might shed light on the zoogeographic relationships of the *Megaxyela* species of the Old and the New World.

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